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SERVICE



BREEDING INSECT AND DISEASE RESISTANT FOREST TREES

Proceedings of Servicewide Genetics Workshop

Eugene, Oregon

July 19 - 23, 1982

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Breeding

Resistant

Insect

Forest

and

Diseases

## ACKNOWLEDGMENTS

The Genetics Workshop on Breeding Insect and Disease Resistant Forest Trees was hosted by Region 6, USDA Forest Service, July 19-23, 1982 in Eugene, Oregon. The Willamette National Forest and Dorena Tree Improvement Center staffs did an excellent job making local arrangements and coordinating the field trip and barbecue. Our special thanks go to Pete Theisen, Chuck Gansel, Safiya Samman, Bob Sanders, and Phil Jaspers for their efforts in coordinating workshop activities. We also acknowledge Ray Hoff, GERAL McDonald, and Pete Theisen for their help in developing the workshop agenda. Finally, we want to commend the speakers and participants for their contributions to making this a successful workshop.

Dick Miller  
Genetics Section  
Silviculture Group  
Timber Management Staff  
Washington, D.C.  
September 1982

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Forest Genetics Workshop  
July 19-23, 1982  
Eugene, Oregon

Monday

8:00 a.m.	Opening Remarks	Bob Sanders
8:15 a.m.	Activity Reviews	Dick Miller
8:30 a.m.	FSM 2475 Draft Revision	Dick Miller
9:00 a.m.	GENESIS	Dick Miller
9:15 a.m.	INFO 990	Dale Gunther
9:35 a.m.	Portable Data Recorders	John Murphy
9:50 a.m.	Break	
10:05 a.m.	Net Retrieval System	Jim McConnell
10:30 a.m.	Overview of S&PF Activities in Tree Improvement	LeRoy Johnson
11:00 a.m.	Overview of Research Activities in Tree Improvement	Ray Hoff
11:30 a.m.	Lunch	
1:00 p.m.	Welcome	Mike Kerrick
1:15 p.m.	Is Resistance Real?	Elmer Johnson
	Moderator - Tom Hofacker	
2:15 p.m.	Literature Review of Insect Resistance in Forest Trees	Sharon Friedman
3:00 p.m.	Break	
3:15 p.m.	Resistance in Ponderosa Pine to Bark Beetles	Dick Smith
4:00 p.m.	Resistance in Douglas-Fir to Spruce Budworm	Geral McDonald
4:15 p.m.	Spruce Budworm	Gary Pitman

## AGENDA (cont'd)

### Tuesday

Moderator - Dick Jeffers

#### Description of NFS, S&PF, and Research Pest Resistance Programs

8:00 a.m.	PSW	Bro Kinloch
8:30 a.m.	R-5	Jay Kitzmiller
9:00 a.m.	INT	Ray Hoff and Gerald McDonald
9:30 a.m.	BREAK	
9:45 a.m.	R-1	Jerry Franc
10:15 a.m.	R-6	Safiya Samman
10:45 a.m.	PNW	Roy Silen
11:15 a.m.	R-9	John Murphy
11:45 a.m.	LUNCH	

Moderator - George Howe

1:00 p.m.	SO	Cal Bey
1:30 p.m.	SE	John Kraus
2:00 p.m.	R-8	Jim McConnell
2:30 p.m.	Bent Creek, S&PF	Bob Anderson
3:00 p.m.	Break	
3:15 p.m.	Table--Rust Resistant Mechanisms	Dick Miller
3:45 p.m.	Rust Races-- <u>C. fusiforme</u>	Harry Powers
4:30 p.m.	Rust Races-- <u>C. ribicola</u>	Gerald McDonald

### Wednesday

Moderator - Ralph Lewis

8:00 a.m.	What Can be Learned From Agricultural Resistance Breeding Programs	Ray Hoff
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# AGENDA (cont'd)

8:30 a.m.	Selection Methods--Vertical Resistance	Bro Kinloch
9:00 a.m.	Selection Methods--Horizontal Resistance	Ray Hoff
9:30 a.m.	BREAK	
9:45 a.m.	Progeny Tests-- <u>C. fusiforme</u>	Cal Bey
10:15 a.m.	Progeny Tests-- <u>C. ribicola</u>	Safiya Samman
10:45 a.m.	Seed Orchards-- <u>C. fusiforme</u>	Harry Powers
11:15 a.m.	Seed Orchards-- <u>C. ribicola</u>	Jerry Franc
11:45 a.m.	LUNCH	
12:30 p.m.	Field Trip to Dorena Tree Improvement Center	Pete Theisen

## Thursday

Moderator - LeRoy Johnson

8:00 a.m.	Maintaining Genetic Variation in Resistant Populations--How Much Variation is Necessary?	Ralph Lewis
8:30 a.m.	Hazard Alignment--INT	Geral McDonald
9:00 a.m.	Hazard Alignment--R-6	Jim Hadfield
9:30 a.m.	Fusiform Rust Hazard in Southern U. S.	Ron Froelich
10:00 a.m.	BREAK	
10:15 a.m.	Concepts of Adaptation as it Applies to Oak-Pine Rust	Glen Snow
10:45 a.m.	Impact of Native Insects in Off-site Plantations	Roger Sandquist
11:15 a.m.	Impact of Native Diseases in Off-site Plantations	Jim Hadfield
11:45 a.m.	LUNCH	
1:00 p.m.	Genetic Gains Realizable in Rust-Resistance Programs--What are We Buying	George Howe



AGENDA (cont'd)

1:30 p.m.

Panel Discussion--Leader

Ed Wicker

Opportunities for Using Natural  
Resistance and Resistant  
Genotypes in Forest Management.  
(Will include IPM Decision Key--  
SA, S&PF.)

Pete Theisen,  
Bob Anderson,  
Gerald McDonald, and  
Harry Powers

# ATTENDEES

George Howe	Regional Geneticist	R-1 Missoula, MT
Gerald Franc	Breeding Specialist	R-1 Moscow, ID
Suzanne Dubreuil	Pathologist	R-1 Missoula, MT
Gary Manning	Silviculturist	R-1 Wallace, ID
Dick Jeffers	Regional Geneticist	R-2 Denver, CO
Ken Ready	Regional Geneticist	R-3 Albuquerque, NM
Orville Engelby	Regional Silviculturist	R-4 Ogden, UT
Jay Kitzmiller	Regional Geneticist	R-5 Chico, CA
Roy Sharp	North Zone Tree Improvement	R-5 Yreka, CA
Dean Davis	North Zone Tree Improvement	R-5 Happy Camp, CA
Pete Theisen	Regional Geneticist	R-6 Portland, OR
Jim Hadfield	Pathologist	R-6 Portland, OR
Roger Sandquist	Entomologist	R-6 Portland, OR
Charles Gansel	Dorena Tree Improvement Center	R-6 Cottage Grove, OR
Safiya Samman	Dorena Tree Improvement Center	R-6 Cottage Grove, OR
Jim Hamlin	Area Geneticist	R-6 Roseburg, OR
Sharon Friedman	Area Geneticist	R-6 Lakeview, OR
Bill Randall	Area Geneticist	R-6 Corvallis, OR
Carol Apruzzese	Forest Geneticist	R-6 Seattle, WA
Sheila Martinson	Forest Geneticist	R-6 Vancouver, WA
Don Oliver	Forest Geneticist	R-6 Corvallis, OR
Tom Tibbs	Forest Geneticist	R-6 Grants Pass, OR
Dale Guenther	Computer Specialist	R-6 Idleyld Park, OR
Phil Jaspers	Silviculturist	R-6 Eugene, OR
Bob Sanders	Silviculturist	R-6 Eugene, OR
Jim McConnell	Regional Geneticist	R-8 Atlanta, GA
Ralph Lewis	Zone Geneticist	R-8 Atlanta, GA
Jim Gates	Zone Geneticist	R-8 Pineville, LA
John Murphy	Regional Geneticist	R-9 Milwaukee, WI
Dick Meier	Zone Geneticist	R-9 Rhinelander, WI
John Gronquist	Project Geneticist	R-9 Lakewood, WI
Bob Anderson	Pathologist	R-8 Asheville, NC
John Brissette	Nursery Specialist	R-8 Jackson, MS
LeRoy Johnson	Geneticist	NA St. Paul, MN
Ray Hoff	Research	INT Moscow, ID
Geral McDonald	Research	INT Moscow, ID
Mel Morton	Research	INT Moscow, ID
Roy Silen	Research	PNW Corvallis, OR
Richard Smith	Research	PSW Berkeley, CA
Harry Powers	Research	SE Atlanta, GA
John Kraus	Research	SE Macon, GA
Calvin Bey	Research	SO Gulfport, MS
Glen Snow	Research	SO Gulfport, MS
Ron Froelich	Research	SO Gulfport, MS
Liang Hsin	Geneticist	BLM Portland, OR
Gary Pitman	Professor	OSU Corvallis, OR
Dave Nielsen	Graduate Student	OSU Corvallis, OR
Elmer Johnson	Geneticist	San Carlos, CA
Tom Hofacker	Entomologist FPM	WO Washington, D.C.
Ed Wicker	Research	WO Washington, D.C.
Dick Miller	Geneticist	WO Washington, D.C.

OBJECTIVES OF THE GENETICS WORKSHOP ON  
BREEDING INSECT AND DISEASE RESISTANT FOREST TREES

Dick Miller

I would like to welcome all of you to Eugene and this workshop on breeding forest trees for insect and disease resistance. I am especially pleased to see the large number of representatives from Research and State and Private Forestry. We look forward to your participation.

Four objectives have been identified for the workshop. The first, and perhaps most important, is to discuss the development and use of disease resistant forest trees. Servicewide, significant investments are being made to develop and test resistant trees: four Research Stations, Intermountain, Pacific Southwest, Southeast, and Southern, have active research projects; Forest Service Regions 1,5,6,8, and 9 have implemented special tree improvement programs; and State and Private Forestry, Region 8, is operating the Bent Creek Fusiform Rust Test Center at Asheville, North Carolina. This workshop will provide the opportunity to become more knowledgeable about current research programs and results, and the strategies being used by the various Regions to develop disease resistant trees.

The speakers who have prepared papers describing Region, State and Private, or Research resistance programs were given a list of topics to address. This should make it easier to compare how specific tasks are performed in the various programs. These papers will be presented on Tuesday.

The second objective is to identify and describe resistance mechanisms. Data gathered prior to the workshop will be presented and an attempt will be made to develop a common terminology and description for each mechanism (or host response).

A third objective is to provide an overview of research being conducted on insect resistance in forest trees. This is a relatively new area of research that could have significant impacts on future tree improvement programs. These papers will be presented this afternoon.

The fourth objective is to visit the Dorena Tree Improvement Center and see the techniques being used by Region 6 in their resistance breeding work. This will be an excellent opportunity to discuss and compare your techniques and strategies with those used in other Regions.

This morning we will be discussing several topics of general interest including tree improvement activity reviews, FSM 2475 draft revision, the genetics information system (GENESIS), use of INFO 990 data base management system for tree improvement data, use of portable data recorders, use of the net retrieval system for seed collection, and overviews of Research and State and Private Forestry activities in tree improvement.

Finally, I ask the speakers to please stay within their allotted times. Discussions will be held after each paper as time permits. I encourage all of you to participate in the discussions.

## IS RESISTANCE REAL?

ELMER C. JOHNSON

Plants feed the world. Plants provide much of our shelter. Plants of previous times and their accumulated sun energy in the form of fossil fuels drive much of the machinery of our present civilization. All animal life ultimately depends on plants, and it certainly behooves man to manage his environment in such a way as to provide for a continual healthy existence of the other organisms upon which he depends for his own well being. We are hearing more and more these days about ecology and what is vaguely called the balances of nature as people become more aware of and concerned about what is happening to the earth and its living inhabitants.

When man - or was it woman? - discovered how to plant and grow his own food from a few species that were especially well suited to providing a predictable and controllable supply of things to eat, we had the beginnings of agriculture and the basis for enormously increased population. Now hunting, fishing and picking wild berries are recreational activities that we try to enjoy instead of the basic means of survival that they once were. We are engaged in major industries called agriculture and forestry from which we expect to obtain the essentials of a dependable food supply and the structural materials, drugs, drinks, flavorings, fibers and miscellaneous chemicals used in providing the comforts and conveniences of an increasingly large and demanding society.

In the process of the development of these pursuits we have accumulated a tremendous amount of information about the conditions under which plant and animal species prosper or are endangered and about the complexity and interdependence of life forms. All of us here are involved in one way or another in the continuing changing of the kinds and amounts of living things that inhabit the earth. The total changes since man began to plow up grasslands and cut down the forests are

staggering. The millions of hectares that are annually plowed up and planted to enormous populations of our major crops in carefully controlled fields are a long way removed from what the surface of the earth once was. Forestry is more and more concerned about managing trees as a crop on a permanent basis. I have been told that much of the Mediterranean Sea was once bordered by coastal forests that were cut down to build ships, houses, and to provide fuel. There are no forests there now, and we see other areas of the world being skinned off that future generations will be unable to visualize as having once been forests. We have made, and are continuing to make, massive changes in the numbers of plants of certain species that occupy the surface of the land with the corresponding changes in other organisms that are either favored or limited by those changes.

It is no simple matter to reverse the process, nor is it at all clear what the eventual consequences will be, or that everything that has been done is all bad. Our accumulated conclusions from studies of history indicate that even before man began to be a major factor in the environment that change was certainly going on. The present power of man to modify environment and his demand for more and more food are not likely to lead us to abandon agriculture and forestry and go back to hunting, fishing and picking wild nuts and berries for food. More than 200,000 plant species have been classified, but only about 300 or so have been cultivated to any degree. Of these, perhaps a dozen provides 95% of the total world food supply. The grass family by itself is estimated to produce 75% of the world's food supply (Anderson 1952). As we make larger and more dense concentrations of particular genotypes of plants we are providing ideal conditions for the multiplication of those organisms which find that particular habit suitable for their own development. The interdependence of organisms is both an asset to man and a source of considerable inconvenience. Among the smaller life forms we have isolated certain ones and put them to use making wine, beer, yogurt, cheese, antibiotics and other products for our convenience. Not all the organisms that exist are regarded with quite so much favor, however, as some obtain their food supply from plants in such a way as to reduce the yield of a wheat crop, rot the peaches, kill the elm trees, or blight the leaves and stalks of the corn crop.



When plants exist in mixed stands with other different kinds of plants they provide less than ideal conditions for any one special kind of organism which lives upon it or within it to multiply. But as we crowd more and more similar plants together, the opportunity increases for those particular organisms to prosper and increase. Essentially this is what we do when we put genetically uniform varieties into dense stands and in large acreages. Multiline wheat varieties containing different genes for rust resistance in that crop (Borlaug 1958) have been proposed as one practical control method for stem rust. A great deal has been said and written on the subject in the last few years in calling attention to the need to preserve our resources of genetic variability in our crop plants, for it is the genetic plant variability that is the building blocks from which we organize directed evolution to give us the varieties that are of high and dependable yields. Of course, the micro-organisms also are blessed with genetic variability and can recombine in parallel ways to frustrate our efforts. Plant breeding (Stakman and Harrar, 1957) to keep always a step ahead of the micro-organisms with resistant varieties, still remains the cheapest and most satisfactory control for many diseases. Those of us who are devoting our careers to this field find this a comforting statement in that our services are unlikely to become obsolete in the near future. But I would like to talk specifically about corn.

Corn (Zea mays) is one of the three most important plant species upon which man depends either directly or indirectly for his food supply. Grain is consumed directly as human food; it is converted through feeding into animal products for human consumption; it is processed into an increasing array of starches, edible oils, sweeteners, and other derivatives.

Corn has become a major crop on all the continents of the world, and probably is cultivated over a wider range of ecological conditions than any other crop species. It is grown in equatorial regions and as far north as Alaska, and from sea level to 14,000 feet elevation. Yet the plant appears to be dependent on man for survival, for without the intervention of man in harvesting, storing and planting the seed there

would be no corn. At this time there is not any known corn growing anywhere in the world under native plant stands nor are there any written records of it ever having done so. Its origin remains obscure, but its utility in serving the needs of man is remarkable.

In the process of evolution that has occurred in the maize plant as man has preserved those variant types which most nearly suited his needs under widely different growing conditions and for different characteristics of the grains, a myriad of varieties has developed. Many of these have been collected and put in germplasm storage banks. The task of sorting out which ones are best suited to which areas and to what kinds of cultural and harvesting practices has become a major one. Many of the types that have evolved in small plantings in subsistence type farming are unsuitable for production under intensified and more mechanized managements, so that the plant characteristics must be modified to meet these changed conditions. The genetic manipulation of the heritable traits of plant height, standability, maturity, tolerance to the field hazards of diseases and insects, the color and texture of grain plus other traits is a complex and expensive undertaking.

Maize grain yields in the tropics and sub-tropics of the world compare unfavorably generally with those obtained in temperate regions. Yields of 10 tons per hectare on commercial acreages such as are frequently obtained in temperate regions (Frey 1971) simply are not to be found in lowland tropical areas. Yields of 5 to 8 tons of grain per hectare are about the best that can be obtained, and these are uncommon. Higher yields obtained in the tropical latitudes (Allison 1969, Harrison 1970) have been confined to intermediate and higher altitudes characterized by long growing seasons and cooler night temperatures.

While it is true that erratic moisture supplies, insect and disease problems, poor soil fertility and other environmental factors all take their toll on grain yields in the tropics, it cannot be said that eliminating these through the application of irrigation, fertilizers and pest control will result in grain yields equal to those obtained in temperate climate conditions. Repeated attempts have demonstrated that

it simply doesn't happen, but no clear explanation has been presented that adequately accounts for the discrepancies.

Photosynthetic studies estimating the efficiency of conversion of visible radiation into dry matter for tropical maize (Goldsworthy, 1974) gave a range of 5.1 to 7.2 percent, while studies for the U.S. Corn Belt (Stewart, 1974) were reported at from 4.7 to 6.4 percent. More specific information detailing the distribution of the dry matter in the form of grain vs. non-grain in different genotypes of tropical and temperate origin has been provided by workers in Mexico (Goldsworthy and Colegrove, 1974; Goldsworthy et al., 1974; and Yamaguchi, 1974a, 1974b) who noted the lower percentage of grain produced by the tropical maize when compared to types of temperate regions origin, suggesting background genetic differences. At least part of the differences between the tropical and temperate corns in their respective habitats might be attributed to the ratios of daylight to dark hours and the resultant net accumulation advantages under the long days in the temperate latitudes. Further studies reported levels of soluble sugar in the stems of 1,250 kilograms per hectare in tropical corns compared to 250 kg/ha for temperate material (Fisher and Palmer, 1980) where grown under the same conditions, further supporting the concept of genetic differences.

All this would appear to suggest that the solution to low grain yields of corn in the tropics is to substitute the temperate germplasm for the inefficient grain-producing tropical types. There have been many attempts to do exactly this, and they provide some spectacular illustrations of the answer to the question I was asked to use as the title for this talk. There are special environmental situations of low relative air humidity where irrigation water is available during the cooler season of the year where good yields can be obtained under excellent husbandry conditions for the crop, and measurements can be made such as those referred to in the studies just mentioned. It should be pointed out, however, that no such results have been obtained under the humid lowland conditions where corn must be grown under rainfed conditions. Here is where the temperate background germplasm has proven so sensitive - susceptible, in other words - to the diseases and insects

that normally exist that it is simply impossible to use. Many plantings never reach maturity, but are killed outright before producing any grain. The particular diseases and insects involved vary from one area to another according to the ecological characteristics. Helminthosporium maydis occurs throughout the tropics, and is severe in the lowland humid areas where temperatures are high (it is commonly called "southern leaf blight in the United States). It is unimportant in the intermediate and highland areas where night temperatures are cooler. The opposite case is true of Helminthosporium turcicum, which is severe in the cool and humid highlands, but is unimportant under hot lowland conditions (it is commonly known as "northern leaf blight in the United States). Similarly, Puccinia polysora is a serious problem in the lowlands and of no importance in the highlands, while Puccinia sorghi is serious in many highland areas and of no consequence in the lowlands. These examples are only a few that can be cited of a long list of similar climatic distributions of diseases in which the pathogens very obviously have a range of conditions under which they do well and others under which they do not. Breeding for resistance to such diseases obviously requires conditions suitable for the pathogen to grow well, for in the absence of the disease there is no way to detect differences among the genotypes of the crop plant under selection. It would be nice to have dependable laboratory chemical evaluation procedures.

It is to be expected that the races of corn that evolved in each of these two general categories of highlands (cool) and lowlands (hot) tend to be quite tolerant (resistant, if one cares to use such terminology) to the diseases normally occurring in its area. It is also true that all the highland evolved germplasm tends to be susceptible to the disease problems in the lowlands, and all the lowland evolved germplasm tends to be susceptible to the diseases in the highlands. It has been my observation that all the temperate latitude origin material is susceptible to the disease and insect problems of both the tropical lowlands and highlands.

In trying to analyze where to begin in producing higher corn grain yields in the tropics, the complete unsuitability of the introduced

temperate latitude materials is discouraging. The greater proportion of grain in the total dry matter production (harvest index) of temperate corn types can be expressed in other ways. Morphologically, the tropical corn materials tend to be taller and leafier with bigger tassels and later in maturity. Arguments have been advanced that these traits have been advantageous in the evolution of corn in the tropics as means of survival against the disease and insect depredations and as competitive value against weeds. Mortimer and Ward (1964) suggested that the sugar reserves in the stems were associated with resistance to stalk rots.

Intensified agronomic practices of higher fertilizer levels and more plants per unit of land area with the tall leafy tropical corns simply exaggerated lodging of the plants and as a result actually reduced the recoverable grain yield in some trials. But at least they grew and tolerated reasonably well the complexes of diseases and insects. It was decided to use the tropical materials and to reduce the plant height somehow so as to achieve manageable plant sizes.

Initially, there appeared to be at least three different approaches that might be used to develop corn varieties of shorter stature: 1) Convert materials to the known genetic dwarf mutants such as brachytics 1, 2 and 3, anther ear, dwarf 1 short, compact, etc. 2) Conduct recurrent selection for shorter plants within a population and 3) Cross to shorter materials (including temperate germplasm) and then follow a backcrossing program of selecting for shorter plants in segregating generations with the short plants systematically crossed back to the tall parent and then repeating the procedure. All three of the procedures were begun in the early 1960's prior to the founding of CIMMYT\*, and many of the resulting populations have become the basic populations of that institution. As was expected, each of the approaches was effective in reducing plant height, but each was also accompanied by its own new problems. In the case of the genetic dwarfs, the recovery of the homozygous recessives gave rapid and dramatic plant height reduction. A backcrossing program

\*International Maize and Wheat Improvement Center, Mexico.



was also required to recover the genotype of the recurrent population and reduce the mixture introduced from the genetic dwarf stock to a minimum. Subsequently, it was discovered that the shortened brachytic 2 populations (the best of the genetic dwarfs) did not tolerate higher plant densities than its parent population, and required further modification. The crosses to shorter materials, including temperate types, resulted in substantial changes in the characteristics of the populations including disease susceptibilities brought in by the temperate germplasm. The recurrent selection within populations appeared at first to offer only minor changes in plant height, but now cumulatively has proven to be probably the most significant and useful. Right here I would like to emphasize the importance of the first step in any breeding program: choose the best possible parental materials that can be obtained.

General observations and systematic yield trials over a period of years indicated that the corn race Tuxpeno (Wellhausen et al.) is the most productive and widely adapted of the lowland tropical types. A broad genetic base made up by compositing 15 of the best performing collections as determined by their performance per se and in crosses was used to initiate the selection for shorter plants (Tuxpeno Crema I). The base population had been intermated for several generations before selection pressure for plant height was set as first priority. The selection procedure adopted was a visual one initiated with 400 open pollinated ears that were planted ear to row. At flowering time the ear shoots were covered with glassine shoot bags to prevent uncontrolled pollination, and the 400 families were classified as to being either of less than mean height or above mean height resulting in approximately a 50-50 division. The classification decision was made on each family based on its height in comparison with the two family rows immediately adjacent on both sides, so that in effect a running average was used to avoid the confusion that often results in measuring the plant height under local varying soil conditions in different parts of the nursery. Within each of the 200 selected shorter families, the shortest healthy looking four or five plants were then each crossed to a similarly selected plant in an equal number of similarly selected rows.

This procedure generates about 1,000 pollinations of plant to plant crosses which, when planted again ear to row, establishes a new set of full sib progeny with which to repeat the process. The entire nursery is harvested and the ears produced by each family are laid out in front of the row of plants which produced them, with each ear of the labeled crosses of the hand pollinations carefully identified. A random distribution of the families is maintained in the nursery, and a similar evaluation to that made at flowering is made of each family at harvest. Visibly inferior families and all their crosses can be culled out until approximately the same number of ears remain as the number of family rows that were planted in the nursery. Thus a selection for standability, diseases, apparent yield and other factors can be exercised at harvest within the array of plants selected for shorter plant height. This procedure has been completed for 20 generations now, and performance data of the resulting populations have been compiled.

In brief, what has happened is that the mean plant height was reduced in essentially linear fashion, days to maturity were similarly reduced, as were internode number and internode length. For all practical purposes, lodging became unimportant, and recoverable grain yield was increased substantially. Estimates of genetic variance for plant height comparing cycles 0, 9 and 18 (Moshi 1982) indicated (Table 3) that apparently very little reduction in variance has taken place and that further progress in reducing plant height is possible. Cycle 18 is approximately 50% as tall as cycle 0. Experiment station data for plant height, grain yield, lodging and optimum density (calculated from trials conducted at multiple densities) are shown in Table 1. Relative performances remain similar when compared under different levels of fertilizer, weed control and drought (Table 2), confirming the plant height reduction and the grain yield advantage of the short plant selection.

Morphological data for three locations and two years of evaluation (Tables 4, 5) show that as the plants became shorter with the reduction in node length and number of nodes that they also became earlier to flowering and that the interval between silking and pollen shed was

reduced. Total dry matter produced per hectare (Table 6) did not change in spite of the drastic change in plant size and maturity, so that there was a change in the distribution of the dry matter with a greater proportion in the form of grain in the short plant selection.

The selections for shorter plant height were undertaken in the first place in an attempt to produce plants that were manageable agronomically. The results of greater grain yield from shorter and earlier maturing plants is completely consistent with the experiences with the shorter straw selections of wheat, sorghum and rice. A summary review (Fischer 1976) of yield advances with wheat points out the importance of plant height and harvest index with that crop in Mexico. The concept of recurrent selection and using large numbers of plants to progressively modify the architecture and performance of corn in the tropics have been proposed over the last decade on a number of occasions (Johnson 1976, 1979, Villena, 1972). An analysis of the short plant selection, in effect, shows that the plant height reduction is essentially one of selection against stem while attempting to prevent the loss of ear size. Efforts were made to extend the concept to selection for less tassel, less foliage, early maturity and drought resistance independently in different materials.

Cycle 11 of the short plant tuxpeno was chosen as one population from which three sub-populations were derived by selecting for less foliage in one, for less tassel in another and for drought tolerance in a third. A completely unrelated population composited from germplasm from the Caribbean (Antigua-Republica Dominicana) was used from which to derive two sub-populations by selecting independently for less tassel and for less foliage. The composite variety ETO Blanco was subjected to simultaneous selection for less foliage and less tassel. A full sib mating system was used in all cases, and the procedure was carried out exactly as was done in the selection for short plants except in the case of the drought tolerance selection. The selection for drought tolerance was done under controlled moisture conditions during the dry season when there is no rainfall. The full sib progenies were planted with two replications under full irrigation moisture supply conditions and with

four replications under a progressive drought stress. Irrigation was provided at germination to fill the soil to complete water holding capacity, and then no further moisture was supplied in the progressive stress treatment. Data were taken on plant height at different dates, leaf elongation rates, flowering of both male and female inflorescences, leaf burn, and grain yield. Based on these criteria (weighted for grain yield) the superior approximately 30% of the families were identified. Within this array of families identified under stress, those which also produced grain yields above the mean of the families grown under full irrigation were then identified. Thus, those families which performed above the mean under both the full moisture regime and under severe stress were selected to provide the next cycle of progenies. Reserve seed of these families was planted with which to generate a new set of full sib intercrosses among the families with which to repeat the selection process.

Selection in the Antigua-Republica Dominicana population resulted in less leaf and less tassel as measured by leaf length, leaf width and weight of tassel per hectare, as well as a slight shift toward earlier maturity (Table 7). Grain yields per hectare (Table 8) actually increased. Similar changes occurred in ETO Blanco (Tables 9, 10). Total dry matter produced per hectare in the several selections (Tables 11 and 12) was not changed, so that the grain yield increases represent a shift in distribution of the dry matter from non-grain to grain. More efficient genotypes for grain production resulted from the visual selection against the non-grain morphological traits of the plants. The drought selection similarly resulted in gradual improvement of performance of the population under the specific type of progressive stress that was used in the selection process (Tables 13, 14).

In the case of selection for early maturity, a broad genetic pool was established and designated "Compuesto seleccion Precoz," in which a modified ear to row mass selection procedure was employed to exert selection for earlier and earlier maturity. Selected ears were planted ear to row in an isolated plot in which a balanced mixture was made from all the ears to use as a pollen source in every third row as male rows.

Female rows were all detasseled, and when the male rows were about half through the pollen shedding period, all plants were detasseled. At maturity, the earlier maturing plants in the earlier families were saved to repeat the process, taking care to save ears only from sound plants to avoid selection of diseased plants that died prematurely. Maturity, as measured by number of days from planting to flowering, was shifted toward earliness by somewhat more than one day per selection cycle. Plant height was also reduced (Table 15). Grain yield appears to have declined, but trials with higher plant densities to compensate for the reduced plant size have yet to be carried out.

Within the selection for earliness, four sub-selections were defined by the flowering date and the pre and post flowering date and the pre and post flowering segments of the life cycle. Preliminary data would suggest a yield advantage for the selections with the long post-flower pre-maturity segment (Table 16).

In summary, selection has been effective in modifying all the traits that have been used in these selection programs. A quotation from Comstock (1978), in Quantitative Genetics in Maize Breeding, covers it well: "Present insights and evidence from quantitative genetics suggest to me that the greatest present and future need in maize breeding is for sound recurrent selection programs designed to be effective in relation to the long range goal of achieving very high frequencies of the most useful alleles ..... and need larger population sizes than most present programs....." My observations completely support that statement.

Maybe sometimes we get too impatient and expect too much too soon from our studies and work. It was in 1902 (Biffen) that resistance to stripe rust in wheat was reported to be due to a single recessive gene. Increased yields of corn were observed in variety cross hybrids about 100 years ago by Beal, and high yields from the crosses of inbreds in 1905 by Shamel. East and Shull reported that effects of inbreeding and cross breeding in 1907-1912, and the first commercial hybrid (Burr-Leaming) was by Jones in 1917. (Smith 1966). Large scale hybrid corn developed when the techniques and costs of double cross production became standard. Now

the latest figures show that a high percentage of the hybrids being sold are single or modified single cross hybrids. In 1964, U.S. Corn production was about 3 1/2 billion bushels with an average yield of about 62 bushels per acre. The 1981 U.S. corn yield in round numbers were 100 bushels per acre. Where are we going from here?

That report of gene action of a single gene conditioning resistance to wheat stripe rust was 78 years ago. Gradually our store of knowledge is being increased on the fundamental basis of what happens at the genetic and chemical level. In the last few years phytoalexins have been related to plant pathogens and have been defined as antibiotics which are the results of an interaction of two different metabolic systems, the host and the parasite, and which inhibit the growth of microorganisms pathogenic to plants (Muller, 1956). The definition has been changed to "low molecular weight antimicrobial compounds that are both synthesized by and accumulated in plants after exposure to microorganisms (Paxton, 1980). A few years ago there were reports of a substance called DIMBOA as being the explanation for resistance of certain corn genotypes to the European corn borer (Ostrinia nubilalis). More recent reports indicate other genotypes as being equally or more resistant but that no DIMBOA is present. (Sullivan et al.). The literature is full of examples of substances being found in association with specific diseases or situations, but none of these can yet be verified as the specific explanation. So far as I know at this moment there is not one single case of either resistance or susceptibility where the specific chemical reactions involved are known. There are masses of evidence dealing with the defense mechanisms in plants, and probably one of these days the chemistry will be published of an example of a complete integrated chemical reaction process of resistance or susceptibility. But as of now, most of the work is descriptive, circumstantial and presented as correlations or associations of phenomena with the resulting interpretations according to the several points of view of those wishing to offer opinions. A good reference is the book "Active Defense Mechanisms in Plants," 1982, which is the proceedings of a NATO Advanced Study Institute held in Greece in 1981. Meanwhile, we are still waiting for the integrated detail explanations of whole processes, and in that

respect not unlike the situation of the learned blind men in the poem explaining their impressions of the elephant after each had grasped a different portion of the animal's anatomy.

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Table 1 Plant height, lodging, optimum planting density and the grain yield of various cycles of selection for reduced plant height in Tuxpeño Crema I when grown at their optimum density and at 50,000 plants/ha. (Data are the means of two years testing at three locations; Poza Rica, Obregon and Tlaltizapan, Mexico).

Cycle of Selection	Plant Height (cm)	Grain Yield t/ha		Lodging (%)	Optimum Density (plants /m <sup>2</sup> )
		Optimum Density	50,000 plants/ha		
0	282	3.17	3.13	49	4.6
6	218	4.29	4.24	9	5.4
9	210	4.48	4.31	10	5.6
12	202	4.93	4.71	6	5.6
15	179	5.40	5.03	5	6.5
L.S.D. P.05	7	0.32	0.36	12	1.2

Table 2 The effect of selection for reduced plant height in Tuxpeño Crema I on grain yield at various input levels, and on harvest index.

Cycle of selection	Plant height (cm)	Grain yield (t/ha)					Harvest Index
		*optimum conditions	farmer field recommended management	poor weed control	low nitrogen level	drought	
0	273	4.05	3.34	2.23	2.47	1.1	0.30
6	211	5.54	4.16	2.80	3.00	1.2	0.38
9	203	5.67	--	--	--	--	0.39
12	196	6.18	4.34	2.67	2.87	1.6	0.41
15	173	6.73	5.02	3.27	3.30	1.7	0.46
LSD <sub>P.05</sub>	10	0.41	--	--	--	0.4	0.05

\*Mean of two locations (experiment stations) and two years.

Table 3. Components of variance and related estimates for cycles of selection for reduced plant height in Tuxpeno Crema 1.

Trait	Cycle of selection	Variance component estimates			Genetic C.V.	$\sigma^2_{h^2}$ Progeny mean $\pm$
		$\sigma^2_{oe}$	$\sigma^2_{ge}$	$\sigma^2_g$		
Plant height (cm)	C <sub>0</sub>	168.29 $\pm$ 13.34	20.73 $\pm$ 13.01	122.00 $\pm$ 26.25	4.35	76.05
	C <sub>9</sub>	74.27 $\pm$ 5.91	4.35 $\pm$ 5.03	32.62 $\pm$ 7.86	3.54	69.15
	C <sub>18</sub>	38.30 $\pm$ 3.05	16.47 $\pm$ 10.10	64.18 $\pm$ 2.54	6.70	84.39
Ear height (cm)	C <sub>0</sub>	75.98 $\pm$ 6.04	10.11 $\pm$ 5.99	64.80 $\pm$ 13.43	5.30	80.16
	C <sub>9</sub>	34.29 $\pm$ 2.73	5.45 $\pm$ 2.84	20.15 $\pm$ 4.74	5.71	72.65
	C <sub>18</sub>	18.70 $\pm$ 1.49	3.01 $\pm$ 1.55	34.75 $\pm$ 6.31	12.08	89.40
50% pollen shed (days)	C <sub>0</sub>	2.47 $\pm$ 0.20	0.58 $\pm$ 0.23	5.81 $\pm$ 1.04	2.29	90.57
	C <sub>9</sub>	1.31 $\pm$ 0.09	0.40 $\pm$ 0.14	1.17 $\pm$ 0.26	1.13	76.89
	C <sub>18</sub>	1.31 $\pm$ 0.09	0.53 $\pm$ 0.16	3.96 $\pm$ 0.71	2.29	90.93
50% silk emergence (days)	C <sub>0</sub>	4.24 $\pm$ 0.34	1.83 $\pm$ 0.53	6.53 $\pm$ 1.32	2.33	83.22
	C <sub>9</sub>	1.67 $\pm$ 0.13	0.28 $\pm$ 0.14	1.68 $\pm$ 0.34	1.32	81.89
	C <sub>18</sub>	1.66 $\pm$ 0.13	0.52 $\pm$ 0.18	4.61 $\pm$ 0.82	2.44	91.11
Pollen-shed-to-silking interval (days)	C <sub>0</sub>	3.72 $\pm$ 0.30	0.21 $\pm$ 0.31	0.86 $\pm$ 0.24	19.56	54.26
	C <sub>9</sub>	1.55 $\pm$ 0.12	0.03 $\pm$ 0.12	0.68 $\pm$ 0.14	30.43	71.33
	C <sub>18</sub>	0.85 $\pm$ 0.07	0.12 $\pm$ 0.08	0.41 $\pm$ 0.10	52.06	67.03
Grain yield (Mg/ha)	C <sub>0</sub>	0.59 $\pm$ 0.04	0.08 $\pm$ 0.05	0.19 $\pm$ 0.06	16.64	60.00
	C <sub>9</sub>	0.75 $\pm$ 0.06	0.00 $\pm$ 0.04	0.05 $\pm$ 0.03	5.15	26.00
	C <sub>18</sub>	0.43 $\pm$ 0.03	0.13 $\pm$ 0.05	0.15 $\pm$ 0.05	8.09	56.00
Ears/100 plants	C <sub>0</sub>	237.82 $\pm$ 18.92	-2.23 $\pm$ 13.80	155.91 $\pm$ 19.53	16.20	-----
	C <sub>9</sub>	97.02 $\pm$ 7.72	3.30 $\pm$ 6.23	6.58 $\pm$ 4.81	2.83	27.59
	C <sub>18</sub>	30.91 $\pm$ 2.46	7.41 $\pm$ 2.94	4.18 $\pm$ 2.51	2.12	35.42
Root lodging (%)	C <sub>0</sub>	622.82 $\pm$ 49.55	49.54 $\pm$ 44.12	191.46 $\pm$ 54.88	31.69	61.41
	C <sub>9</sub>	12.25 $\pm$ 0.97	2.37 $\pm$ 1.08	2.49 $\pm$ 1.04	108.86	46.79
	C <sub>18</sub>	1.15 $\pm$ 0.09	20.05 $\pm$ 0.08	-0.02 $\pm$ 0.05	94.28	-----
Stem lodging (%)	C <sub>0</sub>	161.55 $\pm$ 12.85	11.38 $\pm$ 11.23	13.25 $\pm$ 8.95	27.55	30.14
	C <sub>9</sub>	15.12 $\pm$ 1.20	-1.67 $\pm$ 0.69	1.52 $\pm$ 0.60	0.61	-----
	C <sub>18</sub>	2.98 $\pm$ 0.24	0.06 $\pm$ 0.19	0.02 $\pm$ 0.12	26.35	3.73

+ Based on 2 environments and 3 replications at each environment.

Table 4 Morphological characters for various cycles of selection for reduced height in Tuxpeño Crema I (Data are the means over three locations in Mexico, Poza Rica, Tlaltizapan and Obregon; Summer 1978).

Cycles of Selection	Days to Flower		Height		Node Number		**LAI	Lodging (%)
	Male	Female	Plant (cm.)	Ear (cm.)	Total	Above Ear		
0	68.7	73.2	293	198	24.9	6.0	4.76	46
6	64.6	67.9	227	138	23.2	6.0	4.64	3
9	64.6	67.4	210	122	23.1	6.1	4.74	3
12	63.7	66.6	205	116	22.6	6.0	4.59	2
15	60.9	62.7	179	99	21.9	5.8	4.12	0
*Check-1	62.3	65.4	213	121	22.8	6.1	4.57	5
L.S.D. P.05	0.9	1.3	8	6	0.5	0.3	0.42	8

\*Check-1 - Population IPTT 21 (C<sub>2</sub>)

\*\* Leaf area index at optimum density, for Tlaltizapan and Poza Rica sites.

Table 5 Morphological characters for various cycles of selection for reduced plant height in Tuxpeño Crema I (Data are the means from three locations in Mexico - Poza Rica, Tlaltizapan and Obregon; Summer 1979)

Cycles of Selection	Days to Flower		Height		** LAI	Lodging (%)
	Male	Female	Plant (cm)	Ear (cm)		
0	66.4	69.5	270	184	4.57	52.8
6	62.8	65.3	212	129	4.96	13.8
9	62.3	64.4	207	113	4.75	18.3
12	61.0	63.5	201	113	4.38	9.8
15	59.6	60.6	182	101	4.39	10.0
17	58.0	58.9	156	80	3.95	7.9
*Check-1	61.0	63.0	195	106	4.64	9.5
Check-2	65.5	67.6	271	173	3.99	36.7
L.S.D. P.05	1.6	1.4	15	13	0.54	14.3

\* Check-1 - Population IPTT 21 (C<sub>2</sub>)

Check-2 - Criollo Alamo

\*\* Leaf area index at optimum density; for Tlaltizapan and Poza Rica sites.

Table 6 Total (above ground) and grain dry matter at maturity and harvest index for various cycles of selection for reduced plant height in Tuxpeño Crema I when grown at near optimum density (Data are for two sites - Poza Rica and Tlaltizapan; Summer 1978).

Cycles of Selection	Total dry matter (Kg/ha)	Harvest index	Grain yield (Kg/ha)
0	15180	0.29	4562
6	15745	0.40	6453
9	16444	0.42	6713
12	16408	0.42	6884
15	16152	0.49	7786
*Check 1	16699	0.43	7205
L.S.D. P.05	1770	0.05	850

\*Check 1 - Population-IPTT 21 (C<sub>2</sub>)  
(Total dry matter x Harvest index = Grain yield)

Table 7 Morphological characters for selection for reduced leaf and tassel size in the population Antigua-Republica Dominicana when grown at 80,000 plants/ha. Data are mean of three locations in Mexico - Poza Rica, Tlaltizapan and Obregon (Summer 1979).

Cycle of Selection	Flowering (Days)		Plant Height (cm)	*Leaf size		+ LAI	Tassel size (at flowering)	
	Male	Female		Length (cm)	Width (cm)		(Kg/ha)	no. branches
C <sub>0</sub>	55.8	58.3	196	73	5.5	3.25	476	18
Reduced leaf C <sub>6</sub>	53.4	54.0	180	70	4.8	2.80	386	13
Reduced tassel C <sub>6</sub>	54.3	54.8	178	70	5.2	2.78	338	9
Reduced leaf C <sub>6</sub> x Reduced tassel C <sub>6</sub>	53.7	54.2	177	69	5.1	2.64	364	11
** Check	53.7	54.7	193	73	5.6	3.28	464	21
L.S.D. P.05	1.2	1.4	14	2.4	0.4	0.28	44	1.1

\* Data from Tlaltizapan only.

\*\* Check - Compuesto Selección Precoz (C<sub>5</sub>)

+ Leaf area index (LAI)



Table 8 Grain yield (0% moisture) at optimum plant density and the calculated optimum plant density for selections for reduced leaf and tassel size in the population Antigua-Republica Dominicana when grown at three sites in Mexico. (Summer 1979)

(a) grain yield

Cycles of selection	Grain yield (Kg/ha)			
	Poza Rica	Tlaltizapan	Obregon	Across sites
C <sub>0</sub>	4366	6741	3512	4873
Reduced leaf C <sub>6</sub>	4405	7398	4535	5447
Reduced tassel C <sub>6</sub>	4256	7530	3764	5183
Reduced leaf (C <sub>6</sub> )				
x	4018	7430	3980	5143
Reduced tassel (C <sub>6</sub> )				
*Check	4028	6314	3836	4726
L.S.D. P.05	387	392	384	252
CV %	6.0	3.6	6.4	---

(b) optimum density

Cycle of selection	Plant density (1000 plants/ha)			
	Poza Rica	Tlaltizapan	Obregon	Across sites
C <sub>0</sub>	74	72	70	72
Reduced leaf C <sub>6</sub>	107	102	67	92
Reduced tassel C <sub>6</sub>	94	105	77	92
Reduced leaf (C <sub>6</sub> )				
x	84	105	64	85
Reduced tassel (C <sub>6</sub> )				
*Check	65	73	54	64
L.S.D. P.05	18	12	12	9

\*Check - Compuesto selección precoz (C<sub>5</sub>)

Table: 9

Morphological characters for various cycles of selection for reduced leaf and tassel size in the population Eto Blanco. (Data are means from three sites in Mexico - Poza Rica, Tlaltizapan and Obregon). (Summer 1979) (Density 80,000 p/ha)

Cycle of Selection	Flowering (Days)		Plant height (cm)	**Leaf Size			** Tassel size (at flowering)**	
	Male	Female		Length (cm)	Width (cm)	+ LAI	kg/ha	no. branches
0	60.2	62.8	205	74.8	5.4	3.39	529	22.9
2	59.3	61.2	208	73.7	5.2	3.17	466	18.8
4	57.4	59.3	202	72.7	5.0	2.92	491	17.9
6	58.5	59.8	195	72.5	4.8	2.56	426	14.0
*Check-1	60.8	63.8	208	76.4	5.5	3.40	489	23.9
Check-2	57.9	59.0	161	72.3	5.3	2.76	550	15.3
LSD <sub>P.05</sub>	1.0	1.1	11	1.8	0.3	0.32	47	2.5

\*Check-1 Population 32 IPTT (C<sub>2</sub>)

Check-2 Tuxpeño Crema I - Reduced plant height (C<sub>17</sub>)

\*\* Data from Tlaltizapan only.

+ Leaf area index.

Table: 10

Grain yield (0% moisture) at optimum plant density and the calculated optimum plant density for various cycles of selection for reduced leaf and tassel size in the population Eto Blanco when grown at three sites in Mexico. (Summer 1979)

## (a) Grain Yield

Cycles of selection	Grain yield kg/ha			
	Poza Rica	Tlaltizapan	Obregon	Across sites
0	4952	5843	3000	4598
2	4552	6065	3340	4653
4	4844	6335	3490	4890
6	5067	6248	3430	4915
*Check-1	4553	5963	2847	4454
Check-2	5268	7196	3287	5250
LSD <sub>P.05</sub>	560	418	457	309
CV %	7.0	4.4	9.4	-

## (b) Optimum Density

Cycles of selection	Plant density (1000 plants/ha)			
	Poza Rica	Tlaltizapan	Obregon	Across sites
0	76	65	55	65
2	70	68	62	67
4	88	69	69	75
6	101	78	70	83
*Check-1	61	62	53	59
Check-2	94	89	53	79
LSD <sub>P.05</sub>	18	15	15	11

\*Check-1 - Population 32 IPTT (C<sub>2</sub>)

Check-2 - Tuxpeño Crema I - Reduced plant height (C<sub>17</sub>).

Table: 11

Leaf area index, total dry matter production and harvest index of various cycles of selection for reduced leaf and tassel size in population Antigua-Republica Dominicana when grown at 80,000 plants/ha at Tlaltizapan. Summer 1979.

Cycle of Selection	Total dry matter (kg/ha)	Harvest index	Grain yield (kg/ha)
C <sub>0</sub>	15,501	.40	6,277
Reduced leaf C <sub>6</sub>	15,037	.44	6,592
Reduced tassel C <sub>6</sub>	16,121	.45	7,217
Reduced leaf (C <sub>6</sub> ) x	15,135	.46	7,008
Reduced tassel (C <sub>6</sub> )			
*Check	14,817	.39	5,745
LSD <sub>P.05</sub>	1,350	0.04	786

\* Check - Compuesto selección precoz (C<sub>5</sub>)

Total dry matter x Harvest index = grain yield.

Table: 12

Total and grain dry matter production and harvest index of various cycles of selection for reduced leaf and tassel size in population Eto Blanco when grown at 80,000 plants/ha. (Data are mean from Tlaltizapan and Poza Rica; Summer 1979),

Cycle of selection	Total dry matter (kg/ha)	Harvest index	Grain yield (kg/ha)
0	13884	0.37	5128
2	14201	0.39	5522
4	14170	0.40	5629
6	13724	0.40	5481
*Check-1	13000	0.30	4787
Check-2	13240	0.45	5986
LSD <sub>P.05</sub>	1430	0.04	489

\*Check-1 - Population 32 IPTT (C<sub>2</sub>)

Check-2 - Tuxpeño Crema I - Reduced plant height (C<sub>17</sub>)  
(Total dry matter x Harvest index = Grain yield).

Table: 13

Coefficient of correlation of the various parameters used for selecting drought tolerant families with grain yield under no-stress and stress (Tlaltizapan 79A).

Variable	Grain yield (non-stress)	Grain yield (stress)
Grain yield (stress)	0.17*	1.00**
Relative leaf elongation rate	0.06	-0.26**
Interval between anthesis and silking (stress)	0.04	-0.36**
Leaf tissue death	-0.15	-0.48**

\* Coefficient of correlation significant P.05  
(N=250)

\*\* Coefficient of correlation significant P.01

Table: 14

Mean performance of the population and twenty best families selected for non-stress and stress conditions (Tuxpeño-1 selection for drought C<sub>1</sub>; Tlaltizapan 79A).

Population and selections	<u>(Grain yield (kg/ha))</u>		Plant height (cm)	Days to flower (50% silking)
	Irrigation	Stress		
Best families (no-stress)	7891	1837	176	86.0
Best families (stress-index)	6854	2549	176	86.9
Population	6314	1654	178	87.6
<u>S.E.</u>	923	550	12	2.8

Table: 15

Comparison of cycles of selection for earliness in Compuesto Selección Precoz (Lote 81) grown at Tlaltizapan 1978 Winter Cycle.

Cycles of selection	Days to flower (50% silking)	Plant height (cm)	Grain yield (t/ha)
C <sub>0</sub>	81.5	199	5.58
C <sub>5</sub>	75.0	182	5.01
Change per cycle (%)	-1.60	-1.71	-2.04
LSD <sub>P.05</sub>	2.95	22.7	0.81



Table: 16

Trends in maturity indices and grain yield after two cycles of selection for variable durations of phenology in Compuesto Selección Precoz (Tlaltizapan 79A).

Seleccion	Days to flower (50% silking)	Maturity index*		
		Grain moisture (%)	Black layer score	Grain yield (kg/ha)
Group 1- Early Flowering Early Maturity	72.5	27.3	92	5276
Group 3- Early Flowering Late Maturity	71.6	29.8	83	5407
Group 2- Late Flowering Early Maturity	75.9	24.1	96	4985
Group 4- Late Flowering Late Maturity	76.6	27.5	92	5567
LSD <sub>P.05</sub>	2.9	--	18	1278

\* Each group harvested 63 days after flowering.

\*\* 100 = max black layer development at harvest.

Insect Resistance in Forest Trees: Can We Use It?\*

by Sharon Friedman

"Ten years ago the forest geneticists available for cooperative work on the genetics of resistance could have been counted on two hands. Today they probably number 50 or more. In ten or more years, several hundred forest geneticists will be available for studies of genetic resistance of trees to forest insects. Besides having more hands to do the job, they will have for study progeny tests and provenance trials already established."

It's certainly difficult to predict the future, but Callaham had some sound reasoning behind these predictions when he made them in 1966. In support of his predictions, he cited the public clamor against the widespread use of persistent insecticides, increasing emphasis on the genetic improvement of forest trees, and the expanding use of artificial regeneration. In the Forest Service, the above factors have increased in importance over the last sixteen years. While we have many geneticists available for such studies, we have very few undertaking them. In this paper, I would like to arouse some enthusiasm in this quarter, and increase the number of forest geneticists at least considering insect resistance activities.

I. Introduction - The Agricultural Experience

Certainly, coordination of activities between geneticists and entomologists is more difficult than between geneticists and pathologists, who generally have the same background in plant physiology. It is also difficult at first to see host resistance as one tool in the integrated pest management toolbox of the entomologist. Yet this situation is advantageous to the breeder, for we do not have to do the whole job - 100 percent of trees may not have to be 100 percent resistant.

On the other hand, resistance to insects has been used as a principle means of control, successfully, in a perennial species. The grape phylloxera has been controlled by the use of resistant grapevines for over 100 years (Painter, 1951). But resistance is more generally used, in agriculture, as an adjunct to other control measures. It may be useful against the insects left after chemical control, or may be useful for a stage of the insect when no other method is viable. An awareness of resistance can also be used to prevent the outplanting of more susceptible material. This may be particularly important in forest trees, where many thousands of acres may be reforested with progeny from a seed orchard. If the progeny are not tested for resistance to an important forest insect, it is possible that the progeny may be more susceptible to an insect than the native tree population, and cause a situation favorable for population buildup. Breeding trees resistant to specific insects may also be a means to decrease diseases transmitted by insects.

\* presented at Forest Genetics Workshop, Eugene, Oregon, July 19, 1982

There may also be relationships between resistant populations of hosts and parasites of insects. These relationships may occur in two ways (Painter, 1951). First, if the level of the insect is reduced, it may be more difficult for parasites to find the insects. Second, changes in the physiology of the insect which result from feeding on resistant plants can affect the parasite favorably or unfavorably. Another possibility is that the attacked plant may itself attract parasites of the insect. Resistance can affect the efficacy of chemical control measures as well. Leafhoppers may be easier to control on host potatoes which are resistant to leafhoppers than on those which are susceptible (Wilson & Slesman, 1947).

Resistance of plants to insect attack has been defined as "the collective heritable characteristics by which a plant species, race, clone, or individual may reduce the probability of successful utilization of that plant as a host by an insect species, race, biotype, or individual" (Beck, 1965). Painter (1951) divided resistance into three main kinds: non-preference, antibiosis, and tolerance. Non-preference is any feature which discourages the feeding, colonization, or oviposition of an animal pest (also called non-acceptance). In antibiosis, feeding on the host plant adversely affects the growth rate or fecundity of the pest. Tolerance does not hinder the colonization, development, or reproduction of the pest in any way. A tolerant plant will grow more normally and produce higher yields than a sensitive (intolerant) plant when they are both infested to the same extent by a pest.

A fourth type of resistance, pest avoidance (Russell, 1978), was included in the term pseudoresistance by Painter (1951). Pest avoidance is the tendency of some plants to avoid infestation because they are not at a susceptible stage when pest populations attack. All or any of these types of resistance can be found in some plant varieties.

## II. Why Trees Are Different

A forest tree is different in many ways from a crop plant. First, as a long-lived organism, a tree is prey to many different insects throughout its lifetime. For example, some insects utilize only mature tree tissue. This can cause practical problems in a resistance breeding program when trees must be grown for thirty or forty years to be tested for resistance. Another problem which occurs due to the long-lived nature of trees is that many generations of insect can occur while the same tree population occupies a site. Therefore, a possibility exists of changes in the insect population to take advantage of any new tree material. This will be discussed later.

Stands of trees are also different from stands of wheat or corn. Stands of trees are usually on sites subject to a high degree of environmental varia-

tion, and in many cases, are on poor quality to downright stressful sites. Amelioration of these problems by cultural practices such as fertilization and irrigation are generally not practical on the wide acreages with low investments per acre of forest lands.

Depending on other constraints, as much as one-half of the trees may be removed in precommercial thinning, before the first commercial entry. Any tree which gets attacked by insects of this part of the tree population is, therefore, not a loss.

Many studies have examined the physiology of the host-parasite interaction. It might be valuable to take a step back from the single host-insect interaction and look at the populations involved (Fig. 1). Basically the insects, parasites, and tree populations are interdependent. We are, in fact, manipulating insect populations by changing the population size, age, and density of a stand whenever we cut trees, and the genetics of the tree population whenever we have a regeneration cut or plant. This situation is extremely dynamic. For example, if all other conditions remain the same and the age of the trees changes (over time) it might be expected to have an effect on the insect populations.

To be more specific, there are four basic types of forest insects (Baker, 1972):

1. Species that damage or destroy the flowers and seeds of trees that are particularly important pests in seed orchards and seed production areas.
2. Species that stunt, deform, or kill young trees by damaging or destroying the terminals, laterals, or roots of plantation trees or natural reproduction.
3. Species that cause loss of vitality, growth reduction, and often death of trees by eating the foliage.
4. Species that feed under the bark or in the wood of living trees and girdle or kill them or riddle them with tunnels.

Besides directly damaging trees, insects can indirectly weaken or kill trees by acting as a vector for fungal, bacterial, and viral diseases.

Some clones in seed orchards have exhibited resistance (e.g., Dioryctria, Merkel et al, 1965; Leptoglossus, DeBarr, 1971) to seed and cone insects. Seed orchards, however, are one of the few places where chemical and biological control are economically feasible. Resistance to cone and seed insects

of clones selected for other traits could be utilized by application of pesticides to clones only for insects to which they are susceptible (DeBarr, 1971).

Defoliators and bark beetles, because of their tendency to epidemic outbreaks, have been the subjects of much study. Silvicultural methods are being suggested as a possibility to maintain populations at endemic levels. For example, in mountain pine beetle, stocking level control and harvest of trees before they become susceptible has been suggested (Pitman, Mitchell and Waring, Pitman and Waring).

In many cases, white fir has been attacked by Douglas-fir tussock moth and western budworm on dry sites, which may have been pine sites before the exclusion of fire (Stoszek, 1977). However, it has also been suggested that defoliator attack may not be a net loss to tree growth; defoliation may actually cause a net increase in radial growth due to nutrient cycling and reduction of competition (Wickman, 1980) (Mattson and Addy, 1975). Stress which allows insect outbreaks to occur may be alleviated by appropriate silviculture. Until the effects of other silvicultural techniques are understood, the applicability of tree improvement to these situations is unclear.

Genetic variation in resistance of forest trees appears to occur for almost all species tested. An excellent review is found in Gerhold (1966). Most of these studies have taken place in provenance tests damaged by insects, and different provenances have shown different levels of infestation. A smaller number of studies have used families within stands or clones and found similar differences in resistance (e.g., Randall, 1971). In general, it appears that there are differences in susceptibility of trees to each insect tested. There is no question that the genetic variation is present in our tree species for some of each of the types of insects mentioned above.

It might be simplest to begin a breeding program for the terminal and root killing group of insects. Variation in susceptibility has been found in such insects as Rhyaciona spp., Eucosma spp., Pissodes strobi, aphids, and midges (DeHayes, 1981; Arru and LaPietra, 1979; Dix and Jennings, 1982; Ledig and Smith, 1981; Kim et al, 1977; Holst and Heimbürger, 1955; Jeffers, 1978; Duffield (in prep). In fact, resistance to this type of insect has been successfully used in a breeding program. The pine reproduction weevil (Cylindrocopturis eatoni) attacks and kills young Jeffrey pine (Pinus jeffreyi) in California. Breeding work against this pest led to the development of a resistant interspecific hybrid to Coulter pine (Pinus coulteri). The backcross to Jeffrey was then mass produced and planted on pine sites where the weevil was a problem (Smith, 1966). It was later discovered that better site preparation reduced the problem so that the resistant stock was no longer necessary.

The advantages of working on plantation insects are that:

- 1) Populations of some of these insects tend to stay at approximately the same levels (trees in field-tests will be exposed to insect attacks relatively frequently),
- 2) material can be tested in the field for a relatively short period of time (generally less than ten years), and
- 3) no other economic method of controlling these pests usually exists.

### III. Resistance-Breaking Biotypes

In breeding for any type of insect, there is the possibility that the insect will adapt to the new types. Russell discussed the agricultural experience with new biotypes extensively (1978).

There are four main types of biotypes of pests in relation to resistant plants:

- 1) True resistance-breaking biotypes are variants which can attack previously resistant varieties;
- 2) unusually vigorous biotypes, which colonize both resistant and susceptible host plants more effectively than other biotypes, but are not specifically adapted to certain host genotypes;
- 3) biotypes which occur in certain geographic areas, regardless of where resistant varieties are grown; and
- 4) resistant varieties may be attacked by pest populations to which they never were resistant, due to misidentification of the pest (Russell, 1978).

Those types of resistance which have been overcome by true resistance-breaking pest biotypes have, almost invariably, been those which are controlled by major genes. Not all types of monogenic resistance, however, have been overcome by such biotypes. Some hypothesized reasons for this include:

- 1) Varieties may not have been widely grown or exposed to pest attack sufficiently for resistance-breaking biotypes to arise;
- 2) resistance-breaking biotypes of some pests may be less likely to occur or to be disseminated than those of other pests; and
- 3) resistance based on morphological features of the plant, such as pubescence or solid stems, appears to be durable (Russell, 1978).

Resistance-breaking biotypes of pests have been generally less of a problem to crop breeders than variants of fungal or bacterial pathogens. One explanation is that some insect pests may not be extremely host-specific, and thus may not be exposed to the same intensive selection pressure as pathogens when resistant material is substituted for susceptible. Insects are quite capable of adapting to new insecticides, but in this case selection pressure is extremely strong. Insects also have behavior which can be changed to adapt to conditions, without requiring genetic change. Another explanation is the difference in number of propagules produced per plant. Pathogens produce millions of bacteria, or sufficient fungal mycelia to produce hundreds of thousands of spores, while insects can generally be numbered in the hundreds per plant (Russell, 1978).

Resistance of crop plants to pests is usually not responsive, and thus the resistance mechanism usually existed in the plant before the pest came into contact with it. Therefore, it may be difficult for insects to circumvent these resistance mechanisms, and these types of resistance may be similar to non-race-specific types of resistance to plant pathogens.

True resistance-breaking biotypes seem to be more common in some insects than others. Hemiptera, especially aphids, and nematodes generally have had more resistance-breaking biotypes than moths and butterflies (Lepidoptera), beetles and weevils (Coleoptera) or sawflies (Hymenoptera). This has been suggested to reflect the specific associations between certain insects (nematodes and Hemiptera) and their host plants (Russell, 1978).

In general, resistant varieties have given good control in the field despite the existence of true resistance-breaking biotypes.

#### IV. Steps to Establishment of a Breeding Program

To illustrate the steps involved in a breeding program, an example of a breeding program for the western pine shoot-borer (Eucosma sonomana) was used. All entomological information was obtained from K. Stoszek (1973 and pers. comm.).

1. Assess the economic importance of the insect damage. For example, damage by the western pine shoot borer was estimated to be \$60 million over a 60-year rotation on 400,000 acres of Weyerhaeuser land in southcentral Oregon.
2. Narrow down the problem. On what sites, to which species, at what age is the damage greatest? For the shoot borer, some ecoclasses were practically free of insects, while other ecoclasses experienced damage in excess of 50-70 percent. If a program is begun for specific sites, then another economic analysis would be useful including only those sites.

3. What are other control measures? For the shoot borer some alternatives are pheromone mating disruption or planting other species. On the most troublesome sites for ponderosa pine, only ponderosa pine will grow, however. Genetic resistance would have an advantage of not requiring repeated applications over time; resistant seedlings could be planted with no or fewer extra visits for insect control required on the plantations. The shoot borer is a problem on ponderosa and lodgepole pines between 1.5-45 meters tall.
4. Assimilate information on the targeted insect: ideally, distribution, life cycle, population dynamics, mutability, age, and kind of trees attacked, alternate or less preferred hosts, attack habits, damaging stages, and susceptibility to chemical and biological control (Callaham, 1966). In western pine-shoot borer, populations have been found to be stable and low - a few hundred insects per hectare and no fluctuation greater than 50 percent from one year to the next.
5. Decide on testing. Field testing has the advantage that all the factors in Figure 1 which influence the host population are integrated. Also, already existing progeny tests can be used if insect infestations are present. An advantage of field testing is that if a clone is resistant to the primary insect pest and less resistant to another insect, there is a possibility that this will be picked up by the test. The problem with field tests, however, is that environmental variability may obscure the results.

Cage testing can pick up some types of resistance, but not all types. It may be faster than field testing. However, it cannot test for all the conditions present in the field. Indirect selection may be used in cases when resistance is tied to a readily observable morphological or biochemical feature. Selection of material for testing can be done among those families expressing resistance in wild stands or in progeny tests.
6. Decide on breeding scheme. Probably will be the same as used for other economic traits.
7. Use resistant materials.

Very little, if any, empirical data are available on how best to use insect resistance in forest trees. Different lines can be bred, each of which has a single gene for resistance, and mixed in plantations. Different resistance mechanisms can also be combined in the same line. A problem with these approaches is that a super-race of pest might be able to build up over time and attack all resistant lines.



Based on work with the southern pine beetle (Namkoong et al, 1979), the way to keep small, endemic populations is to diversify stands as much as possible spatially and temporally. Both species and within-species variation can be used to aid in this diversification.

For some insect species which are adapted to a low density of preferred shoots on a site, such as western pine-shoot borer (or preferred types of trees, such as mountain pine beetle), an alternative strategy may be to use what I shall term "insect-stabilizing" resistant populations. This is an attempt to keep insect populations stable in size and genetics by causing selection to favor no change from the biotypes presently adapted to populations. For example, say an insect is adapted to finding around 30 percent preferred shoots in a host population each year; if it doesn't find any preferred shoots, genetic selection will operate strongly. It is likely that if in a plantation the insect population finds between 30 and 100 percent preferred shoots, selection will not operate on the insect toward overcoming resistance in the trees. There should be a theoretical point then, a ratio of susceptible to resistant material, which may allow the long-term stability of this system as much as is possible.

If tolerance resistance mechanisms are present in the resistant material, which by definition do not affect the success of insect populations, part or all of the 30 percent expected to be eaten could be composed of tolerant plants. If done properly, this should produce a high-yielding tree population with little risk.

The success of outplanting resistant material will depend on the composition of the resistant plantation relative to that of surrounding stands, throughout the time when the plantation could be damaged. If, as on high-site land, all acres are to be planted within this time period, there are two possibilities. One is that resistant material planted all over the landscape will keep insect populations down to a point where they cannot adapt to the resistant material. This seems to work frequently in crop plants, as described above. The alternative is to use insect-stabilizing resistant populations, to keep the insects around, but try to prevent them from undergoing selection to overcome resistance. In plantations surrounded by natural stands, the chance of decreasing the insect populations is not strong, but perhaps the natural stands provide enough habitat that selection would not be strong enough to change an insect population to overcome a certain type of resistance. In this sense, natural stands may have a stabilizing effect on insect populations.

It is clear from this brief discussion that to model the best way to design these populations, more must be known about such factors as

insect migration, flight distances, and host choice. It would also be of interest to know whether annually attacking insects can be effectively encouraged, by the use of resistant material, to attack the same trees every year.

Some of these interactions can be modeled; however, empirical data from field-testing will be needed to test the models. Field-testing incorporates all the factors which may affect tree and insect populations. In some cases, there may be no substitute for planting resistant trees in different configurations, and monitoring the response of insect populations to such changes. Forest geneticists and entomologists should be uniquely suited to this type of research because of the ecological perspective they tend to bring to their work, due to the training in ecology and population biology common in forestry.

The fact that the forest ecosystem is being changed under present conditions by our manipulation of host populations cannot be overemphasized. It seems clear that if we are to disturb the system, we should have enough information to understand the effects of such activities. Breeding for pest resistance, and the knowledge obtained therefrom, may enable us to compensate for changes in the host/insect relationship which we have already caused.

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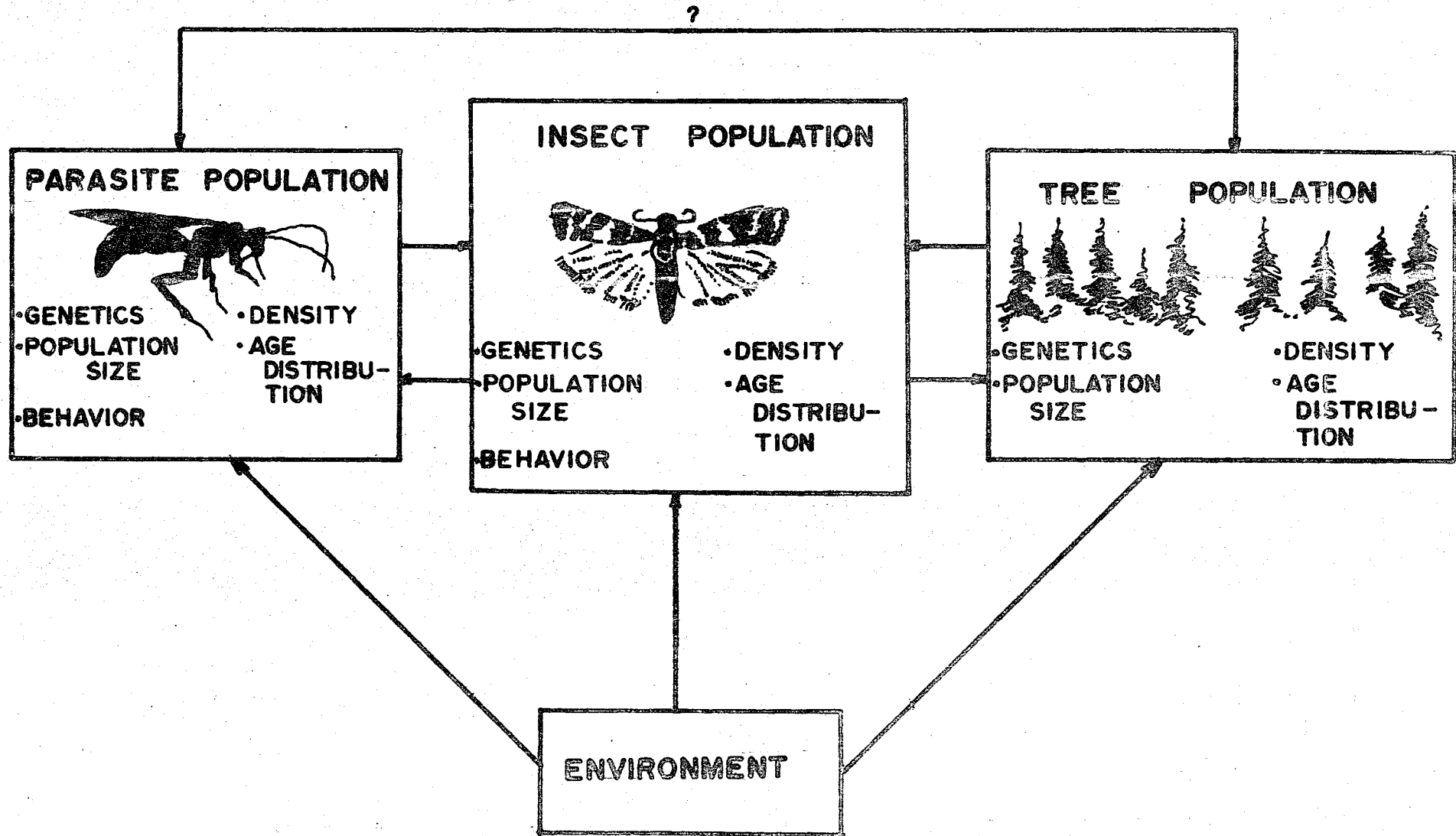


Fig. 1. Some Factors involved in the tree/insect population interaction.

**XYLEM MONOTERPENES OF PONDEROSA PINES: A RESISTANCE  
FACTOR AGAINST WESTERN PINE BEETLE, AND A GENETIC HYPOTHESIS**

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## SUMMARY

Reviews work leading to the development of a working model for resistance of ponderosa pine to western pine beetle: Resistance  $\propto [(resin\ quantity \times resin\ quality) \div (beetle\ quantity \times beetle\ quality)]$ . Observations on a recent epidemic are given to support the model.

Reviews research leading to the development of a working hypothesis for the genetics of the xylem monoterpenes of ponderosa pine: Each monoterpene is controlled by two additive alleles at a single locus, but the amount of each synthesized is dependent on both its alleles and on the alleles of the other monoterpenes which compete for a fixed amount of precursor. Results of recent breeding studies are given to support the hypothesis.

## INTRODUCTION

This report has two sections as noted in the title. Section I describes a preliminary model for the resistance of ponderosa pine (Pinus ponderosa Laws.) to attack by the western pine beetle (Dendroctonus brevicomis Lec.). Section II discusses the derivation of a preliminary hypothesis on the genetics of xylem monoterpenes of ponderosa pine. Each section will present recent research and observations which lend support to the model and the hypothesis.

Research on resistance usually starts with individuals, as is the case for the work summarized in this paper. However, populations of trees are probably more important because it is generally assumed that the interaction between populations of beetles and populations of trees determines whether the beetle becomes epidemic and kill hundreds of millions of board feet of timber or remains endemic and kills only scattered trees. Currently we can only speculate about the effects of populations.

## A RESISTANCE MECHANISM

Background

Only sufficient background review will be given on the interaction of western pine beetle and ponderosa pines to show the development of concepts and programs. Smith (1972) and Hannover (1975) give a more comprehensive coverage of the topic.

Almost from the start of research on forest insects in Western United States, xylem resin was associated with the attacks of bark beetles on pines. Hopkins (1909) concluded, from observations, that until mountain pine beetle (Dendroctonus ponderosae Hopk.) could overcome the flow of resin from ponderosa pine it could not oviposit and thus kill the tree and reproduce. Shortly thereafter similar observations were made about western pine beetle. Mirov (1928) concluded that western pine beetles were most destructive in areas where the resin flow of ponderosa pine was lowest; and Gordon (1932) reported that certain resin components could be toxic to adult beetles. Callahan (1955) found that ponderosa pines judged to be high risk, i.e., most likely to be attacked and killed by western pine beetle, had the shortest period of resin flow. On the other hand Stark (1965) was unable to find a good association between oleoresin exudation pressure and success or failure of western pine beetle attacks on ponderosa pine. Starting in the late 1950's I conducted a series of experiments to determine the direct effect of resin and its monoterpene components on adult western pine beetle (Smith 1963, 1965, 1966, 1969, 1972). Briefly, the results showed (a) that beetles can tolerate host resin vapors significantly better than non-hosts, (b) that vapors of the individual monoterpene components of ponderosa xylem resin varied significantly in their effect on the rate of feeding and in the mortality rate, and (c) that the success of attack depended partially on the monoterpene composition of the xylem resin.

Two more recent studies of stands, rather than individual trees, suggest the operation of resistance at this level. Smith (1977) found that the severity of damage caused by western pine beetle appeared to be related to the average monoterpene composition of ponderosa pine and that distribution of several species of Dendroctonus seemed to coincide with regional types of monoterpene composition. Sturgeon (1979) reported evidence of a shift in the monoterpene composition of a stand that had undergone repeated attacks by western pine beetle, i.e., the level of limonene was, on the average, considerably higher in the residual stand.

#### Forced Attack Experiments To Demonstrate Resistance

Controlled experiments have been done on trees to determine the effects on beetle attack success by three measurable or controllable variables: the amount of resin (quantity), the kind of resin (quality), and the number of beetles (quantity).

The procedure used was as follows (Smith 1966). 30- to 40-year old ponderosa pines were selected on the basis of differing xylem monoterpene composition. A given set consisted of 5 or 6 trees. The basal 12 to 15 ft of the trunk was enclosed with four to five contiguous but separated sleeve cages. The tree above the caged portion was cut off, the flow of resin on the fresh cut cross-section was measured, and a specified number of beetles introduced into the top-most sleeve cage of each of the top-severed trees. After 2 weeks, this top section was cut off and examined for the success of beetle attack as measured by inches of gallery per square foot of phloem. The flow of resin was measured on the newly cut section and beetles introduced into the new top section. This procedure was continued down the trunk.

To a considerable degree, this procedure accounted for three major variables: (a) resin quality was regulated by the selection of trees; (b) resin quantity was partially regulated by the removal of the crown and the

utilization of successive sections of the trunk, since with each of these sections there was generally a reduction in the flow of resin as measured on the newly cut cross section; (c) the density of beetle attack was regulated. But beetle quality could not be controlled.

The data from several sets of experiments were arranged for comparison of the success of attack on pairs of section which were essentially the same for two of the variables but differed in the third variable in order to determine the effect of the differing third variable. Three questions were then asked: How often was success: (a) inversely related to resin quantity, (b) inversely related to the percentage of limonene, and (c) directly related to beetle numbers. The preponderance of positive answers to each question, respectively 17 to 5, 12 to 0, 22 to 1 (Smith 1975), appeared to justify the development of a preliminary model for resistance.

A Resistance Model: The preponderance of positive responses suggested for western pine beetle that: success of attack is directly related to quantity of beetles, and inversely, related to the amount of resin and the percent of limonene. Because of a few negative answers and because most quantitative biological parameters can be modified by quality, beetle quality was added to the model. However, no work has been done on beetle quality. The final generalized formula, where resin quality is percent of limonene, is (Smith 1975):

$$\text{Resistance} \propto \left[ \frac{(\text{Resin quantity}) (\text{Resin quality})}{(\text{Beetle quantity}) (\text{Beetle quality})} \right]$$

The formula thus: (1) provides, at least partially, an explanation for the dynamics of the beetle, (2) can be used by the resource manager to decide the most effective pest management action, i.e what actions can be taken, with the least cost but with reasonable effectiveness, to strengthen the elements in the numerator or weaken those in the denominator; (3) can serve as a guide for

research; i.e. shows where might research be most effective in providing the resource manager with guidelines for decision and methods for action. An example of research is a breeding program started in 1974 to provide plant materials to further test the model.

#### Verification of Model

Recent observation lends support to the validity of the preliminary model. A drought which occurred in much of California in 1976-77 was followed by a return to normal precipitation in 1978.

Entomologists have commonly assumed that ponderosa pines under the stress of drought are more readily attacked and killed by western pine beetle, and that such trees provide a favorable substrate for population increase. In late summer 1977, the mortality of ponderosa pines in the Sierra Nevada and the population of western pine beetle increased sharply. Many trees killed were of smaller size, generally less than 15 inches dbh, and of poorer vigor, as indicated by the smallness of pitch tubes.

In spring 1978, additional large numbers of ponderosa pine were attacked and killed by the overwintering beetle population. By mid-summer larger and more vigorous trees were attacked and killed. But it appeared that more beetles than normal were required to kill such trees. One such tree was a 24 inch diameter tree at the Forest Service's Institute of Forest Genetics at Placerville, California which was being used in a program for breeding for resin quality. The limonene content of the xylem monoterpene was about 25 percent and was considered medium. Western pine beetle attacked this tree in large numbers and the tree was eventually overcome. However, it is estimated that two to three times the average number of beetles was required to kill the tree, and the subsequent brood that developed was 10 to 20 percent of that which might be expected from an average tree. Thus, the ratio of beetles attacking to those emerging may have been as much as 15 to 1. This ratio

would cause a very sharp decline in the epidemic. Somewhat the same general picture was evident in trees with heavy resin flow as indicated by large pitch tubes.

The preliminary model can be applied to the incidence of attack as follows: The first beetles were not successful in attacking the tree because of the strength of both resin quality and resin quantity. But with continued attack by large numbers of beetles, the effects of resin quality and quantity diminished and the tree succumbed. However, the immediate success in killing the tree resulted in a 10- 15-fold decrease in the beetle population.

Though the interaction of ponderosa pine with western pine beetle has an individual tree component, there is, probably more importantly, a stand characteristic. Thus, if beetles attack a stand with a certain frequency of trees with medium or high limonene or heavy flow of resin or both, the beetle population would decline sharply. A stand without these characteristics could result in an increase in the beetle population. This effect is somewhat similar to the removal of high risk trees-- a procedure called "sanitation/ salvage logging" (Salman and Bongberg, 1942). The removal of these high risk trees, generally considered most favorable for population increase, can decrease subsequent beetle losses by more than 80 percent. In sanitation/ salvage the conditions favoring population increase are removed; in the application of the resistance model above, the conditions favoring population decline are enhanced.

## II

### A PRELIMINARY HYPOTHESIS OF THE GENETICS OF MONOTERPENES

#### Background

I proposed a preliminary hypothesis on the genetics of monoterpenes in the xylem resin of ponderosa pine (Smith, 1977). This hypothesis is based on measurements of the inter- and intra-tree characteristics of many trees from

much of the range of the species in Western United States. This hypothesis is based on these observations and results:

- Ponderosa pines growing outside their locality have on the average about the same monoterpene composition as the trees growing at the seed source (Smith, 1977). This similarity suggests that monoterpene composition is under gene control, though one would expect environmental factors to have some effect. This constancy of composition has been found in virtually all pines examined by Forde (1964), Williams and Bannister (1962), Smith (1967), Smith (1982). Their studies covered 35 different species of hard pines and only three failed to have somewhat the same composition as an introduced species as it had as a native. Even the three species that were noticeably different might not be so when better information is obtained about variation in composition in their natural range.
- Within-tree composition of ponderosa pine is quite constant radially and longitudinally (Smith, 1968), and between pairs of forks of the same tree (Smith, 1982).
- The monoterpene fraction of whole resin is quite constant at about 25 percent. In nearly 3,000 trees sampled, about 67 percent had between 22 and 26 percent (Smith, 1977). This condition indicates either that a fixed amount of a precursor is produced or that a feed back regulatory mechanism exists. It also suggests that the monoterpene fraction can be treated as a unit apart from the rest of the xylem resin. Normalization is a most convenient procedure for handling such data, i.e., determining what percentage each monoterpene is of the total monoterpene.
- The distribution of the amount of each of the five major monoterpenes ( $\alpha$ -pinene,  $\beta$ -pinene, 3-carene, myrcene, and limonene) tends to be

trimodal when the amounts in nearly 6,000 trees representing the range in Western United States are plotted. This characteristic is most clearly evident for  $\alpha$ -pinene which has a full range of occurrence of from near 0 percent to nearly 100 percent. It is not as sharply evident in the others probably because the range of amount is not as great. Nevertheless, the trimodal pattern is discernable in selected individual plots of about 80 trees.

- This trimodality suggests two alleles at a single locus with additive properties for each of the five major monoterpenes. Squillace (1976) points out, however, that trimodality does not necessarily result from multigene or multiple allele mechanism. The values to assign to the three levels for each monoterpene were determined by alignment of the frequency distributions. The low interval was given a value of 0, the middle interval 1, and the high interval 2. By using these three values, the composition of a tree can be expressed as a 5-digit figure and classes of trees can be determined and easily handled by automatic data processing. The intervals which were found do not fall into exact multiples, though one fairly clear pattern shows up at the middle level --  $\alpha$ -pinene is about twice as much as 3-carene and  $\beta$ -pinene and four times as much as myrcene and limonene.
- When this 2-allele system is used to code trees with a 5-digit number expressing the three levels of each monoterpene (i.e. a 0, 1, or 2 each for  $\alpha$ -pinene,  $\beta$ -pinene, 3-carene, myrcene and limonene respectively), sets of trees from widely separated geographic locations with the same code values do not differ significantly in actual amounts of monoterpenes despite the large range in values which can be expected. Likewise, groups which differ by only one code value will always be significantly different in the component which is coded differently and will often differ in other components which have the same coded value.



## A Genetic Hypothesis

The preliminary hypothesis on the genetics of monoterpenes may be stated as follows: Each major monoterpene --  $\alpha$ -pinene,  $\beta$ -pinene, 3-carene, myrcene, limonene -- is controlled by two additive alleles, presumably at a single locus. However, since there is a fixed amount of a terpene precursor or a feedback regulatory mechanism or both, the amount of each component synthesized depends on its own pair of alleles as well as on the pairs of alleles of the competing genes of the other monoterpenes. It appears that the pairs of alleles are not equally competitive for the precursor.

### Testing the Hypothesis: Wind pollination

Two types of studies are being used to test the hypothesis: (i) comparative analysis of seedlings of wind pollinated seed, (ii) analysis of seedlings of controlled crosses. The latter is the more desirable; but because of the uncertainty of cone production and the logistic problems in working with selected trees, studies of wind-pollinated seed offered the quickest data.

Wind-pollinated seed were collected from four trees with different monoterpene composition growing at the same locality (table 1). The seeds were planted in the 1972 nursery at the Institute of Forest Genetics. In 1976, xylem resin composition of seedlings of each of the four parent trees was obtained (table 1).

Table 1. Normalized monoterpene composition of four parent trees (P) and the mean composition of their 5-year old wind pollinated progeny ( $F_1$ ).<sup>1/</sup>

Tree Designation		-N-	Monoterpenes				
			$\alpha$ -pinene	$\beta$ -pinene	3-carene	myrcene	limonene
			Percent				
I <u>2/</u>	P	1	21	4	0	15	60
	F <sub>1</sub>	23	17	43	23	2	14
II	P	1	9	30	21	18	21
	F <sub>1</sub>	38	12	48	30	1	5
III	P	1	14	52	0	13	21
	F <sub>1</sub>	33	13	61	15	1	6
IV	P	1	12	57	0	16	13
	F <sub>1</sub>	46	17	55	12	1	4

<sup>1/</sup> Minor components such as camphene,  $\beta$ -phelandrene, and terpinoline not listed but used in normalization computation.

<sup>2/</sup> Classed as a high limonene tree.

The data indicate that the progeny do not have the composition expected and that ponderosa pine seedlings have a period of juvenile instability exceeding 5 years. Thus, the expected xylem monoterpene composition cannot be obtained during this period. This juvenile instability might be related to cortex resin that persists in ponderosa pine for at least 5 years and possibly even 8 to 10 years.

Some preliminary observations can be made during this juvenile period by comparing the ratios of monoterpene components in parents and in progeny from wind pollination (table 2). These comparisons indicate that the comparative level of limonene is about the same among parents and among progeny. Therefore, when the mature composition of the progeny is expressed, it more than likely will be somewhat similar to that of the female parent. These results lend support to the proposed hypothesis.

Table 2. Ratio of limonene in ponderosa pine xylem resin between four parent trees and between sets of their progeny.<sup>1/</sup>

Tree Designation		Tree Number		
		II	III	IV
		Ratio		
I	P	2.8	2.8	4.6
	F <sub>1</sub>	2.8	2.3	3.5
II	P		1.0	1.6
	F <sub>1</sub>		0.8	1.3
III	P			1.6
	F <sub>1</sub>			1.5

<sup>1/</sup> Each value is ratio between parent (P) or progeny (F) of the compared trees.

## Testing The Hypothesis: Controlled Pollination

The monoterpenes composition was determined for the progeny of controlled pollination between parents selected for their composition. The first test (table 3) was done between 2 parents classified as high limonene with little or no  $\beta$ -pinene or 3-carene. The second test (table 4) was done between a tree without 3-carene and three trees with different composition. The progenies were 6 years old. Their resin was prepared and analysed as described by Smith (1982).

All progenies of the high limonene x high limonene cross were also high limonene (table 3). Additionally,  $\alpha$ -pinene was higher than expected while myrcene was much lower. Neither of the two parents, nor the progeny had any  $\beta$ -pinene or 3-carene or only a trace of either. The standard deviations of  $\alpha$ -pinene and limonene were quite high as reflected in the maximum and minimum values for each. These observations suggest that there is a period of juvenile instability in the synthesis of the three components --  $\alpha$ -pinene, myrcene and limonene.

Progenies of crosses of parents with different monoterpene composition (table 4) show the expected qualitative composition but not the quantitative amounts. Again, this suggests juvenile instability. In most cases  $\beta$ -pinene and 3-carene are much higher than expected while limonene and myrcene are much lower -- particularly myrcene.

These experiments provide some evidence to support the hypothesis. Approximate 50 different crosses have been made between ponderosa pines of differing monoterpene composition. The progenies are now in the nursery, containers, or a plantation. Both chemical and biological analysis will be conducted on these in the next 3 to 5 years for further evidence.

Table 3. Normalized monoterpene composition of the xylem resin of two high limonene ponderosa pines (3139, 3298) and the progeny of a controlled cross of the two.

Tree or Function	N	Normalized Composition				
		$\alpha$ -pinene	$\beta$ -pinene	3-carene	myrcene	limonene
		Percent				
3139	1	18	1	*	22	59
3298	<u>1</u>	<u>26</u>	<u>*</u>	<u>*</u>	<u>16</u>	<u>58</u>
$\bar{X}$	2	22	*	*	19	58
F-1 ( $\bar{X}$ )	9	32	2	*	4	60
SD		11.3	0.9	0.6	3.0	11.4
Max.		55	4	2	9	78
Min.		14	1	*	3	37

\* = trace

Table 4. Normalized monoterpene composition of the xlem resin of parents and progeny of 3 sets of controlled crosses, 4B-63 was the female in each cross.

Tree or Function	N	Normalized Composition				
		$\alpha$ -pinene	$\beta$ -pinene	3-carene	myrcene	limonene
		-Percent-				
4B-63	1	9	55	0	12	12
3312	<u>1</u>	<u>5</u>	<u>7</u>	<u>34</u>	<u>0</u>	48
$\bar{X}$	2	7	31	17	6	35
F-1 ( $\bar{X}$ )	11	<u>12</u>	<u>43</u>	<u>21</u>	<u>3</u>	<u>20</u>
4B-63	1	9	55	0	12	22
3352	<u>1</u>	<u>24</u>	<u>0</u>	<u>0</u>	<u>18</u>	<u>57</u>
$\bar{X}$	2	16	27	0	15	39
F-1 ( $\bar{X}$ )	35	<u>16</u>	<u>64</u>	<u>0</u>	<u>2</u>	<u>15</u>
4B-63	1	9	55	0	12	22
3178	<u>1</u>	<u>3</u>	<u>1</u>	<u>55</u>	<u>18</u>	<u>19</u>
$\bar{X}$	2	<u>6</u>	28	28	15	21
F-1 ( $\bar{X}$ )	17	<u>5</u>	<u>36</u>	<u>38</u>	<u>8</u>	<u>15</u>

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# RESISTANCE TO WESTERN SPRUCE BUDWORM

## IN DOUGLAS FIR

by

Gerald I. McDonald

### Introduction

Douglas-fir occupies more land surface than any other species in the northern Rockies and is an important component of stands in many other regions of the West. Without doubt, the most serious pest problem of Douglas-fir in the northern Rockies is western spruce budworm, and the potential for damage is even greater in other regions.

Since populations of a given species are simply large gene pools of indeterminate size, any interaction between populations is ultimately mediated through genetic interaction. Thus, the genetic consequences of every management act must be assessed. The only reasonable approach is to design management alternatives that tend to harmonize the genetic forces rather than to disrupt them.

Genetic variation can be used in several ways. If the resistance traits are strongly inherited and widely distributed in the Douglas-fir population, then stand manipulation can be effectively used. For example, the manager may be able to remove the most heavily attacked trees early in an outbreak and thereby both terminate the outbreak and raise the level of resistance in that stand. Such a stand might also be used as a source of budworm-resistant seed. Depending on the results from this study, other approaches to the use of resistance could be called for. If resistance is scattered or of low heritability, a full breeding program might be necessary to custom tailor Douglas-fir varieties for certain sites, budworm conditions, and package of other control options. Experience with pests on agricultural crops has shown that resistance is seldom the final or only answer, but nearly always it enhances the effectiveness of any other control option. How can forest managers afford to ignore this opportunity for the control of any pest?

The initial step in assessing the role of genetics in such a system is to determine the extent and character of phenotypic variation. The spruce budworm-Douglas-fir system offers plenty of evidence of phenotypic variation (McDonald 1981). The logical next step is to measure the amount of additive genetic variance that could be available to use in some sort of resistance breeding program or as a basis for silvicultural treatments. In order to measure additive genetic variance, progeny test procedures must be perfected. An initial trial proved successful (McDonald 1982); so, an experiment was designed to compare levels of defoliation on progeny obtained from highly defoliated trees growing in a new outbreak with that on progeny obtained from low defoliated trees surviving an outbreak to see if defoliation level was inherited.

This study is designed to answer the following question:

"Is resistance to western spruce budworm in inland Douglas-fir populations under sufficient genetic control to be of value in a breeding program?" This paper addresses the question of larval feeding.

## Materials and Methods

Host materials used were 2-year-old Douglas-fir seedlings obtained from 7 selected parents in each of 4 selected stands.

Stand 1 trees were low defoliated survivors of a high mortality (greater than 60%) outbreak in the Cedar Creek drainage on the Lolo National Forest near Superior, Montana (R27W, T15N, S8&9).

Stand 2 trees were high defoliated individuals from a new outbreak in the Hull Creek drainage on the Salmon National Forest near Salmon Idaho (R20E, T25N, S23&24).

Stand 3 trees were low defoliated individuals from an area of high defoliation of true firs (Abies grandis and A. lasiocarpa) in the Little Goose Creek drainage on the Payette National Forest near McCall, Idaho (R2E, T19N, S23).

Stand 4 trees were low defoliated parents growing in a medium mortality (about 25%) stand in the Grave Creek drainage near Lolo, Montana (R22W, T13N, S32).

Hibernating second-instar budworm larvae were obtained from the Lubrecht Forest about 25 miles east of Missoula, Montana (T13N, R15W, S14), and needle mining second-instar larvae were obtained from Douglas-fir needles located about 9 miles SE of Superior, Montana (T16N, R25W, S13&14).

Larval populations were not sampled in 1980 prior to the main collection. In late April 1980, enough stem length was collected to provide an estimated 5,000 larvae and transported back to Moscow, Idaho and placed in light-proof containers. Traps were affixed to catch the larvae as they broke hibernation and migrated to the lighted traps. In late April the 2,058 Douglas-fir seedlings were removed from cold storage and placed in the test bed.

### Test Procedure

Two cages were constructed to provide 1,044 planting spots each. A 91.4 x 304.8 cm sheet of plywood was drilled with 1,044 2.54 cm diameter holes on a 5.08 cm spacing. This floor was then installed in a 91.4 x 304.5 x 30.5 cm cage made of 32 mesh (32 strands/2.54 cm) nylon screen. The top was totally removable and was held in place by screendoor hooks. This grid was then suspended over a metal tray 91.4 x 304.8 x 15.25 cm. Periodic filling of the tray watered the seedlings from below. The holes were arranged into 58 rows with 18 holes each. Then each spot was designated by row and column. A computer was used to randomize the 74 seedlings from each tree stand combination into 2 completely randomized single-tree-plot blocks (37 seedlings/stand mother tree combination).

As the larvae emerged from their hibernation sites in early May and migrated into the traps, they were placed in small plastic petri dishes, 5 to the dish. The dishes were evenly placed 6 in every other row among the seedlings to give 720 newly activated larvae for replication 1. We had planned the same procedure for replication 2, but we did not obtain sufficient larvae. On May 6, 1980, we collected a large batch of foliage at the second collection site which contained mining larvae. This foliage was placed in light proof containers and the larvae trapped as before. The same procedure was used to distribute the larvae.

The larvae were allowed to crawl from the dishes onto the foliage of the test plants where they developed through the various larval instars to the adult moths. Damage data were collected in August. Length of total foliated and defoliated branch and stem length of 1980 growth on each tree were measured to obtain a ratio of defoliated/total foliated length for each seedling. Analysis of variance were completed according to Snedecor (1956), and family heritability was computed according to Wright (1976).

ANOVA keyout for stand analysis is:

$$Y_{ijk1} = u + A_i + B_{ij} + C_{ijk} + e_{ijk1}$$

where

Y = individual observatioan,

u = general mean,

A = effect of replication,  $i = 1...r$ ,  $r = 2$

B = effect of stands,  $j = 1...b$ ,  $b = 4$

C = effect of families in stands,  $l = 1...c$ ,  $c = 7$

e = error of seedlings in families,  $l = 1...n$ ,  $n = 37$

Heritatility analysis considering random selection of parents and progeny planted in single tree plots is:

$$Y_{ijk} = u + R_i + F_{ij} + e_{ijk}$$

where

Y = individual observation,

u = general mean,

R = effect of replication,  $i = 1...r$ ,  $r = 2$

F = effect of female parents,  $j = 1...f$ ,  $f = 28$

e = error or seedlings in families,  $k = 1...n$ ,  $n = 37$



## Results

Analysis of variance of stands and families (Table 1) shows that family in stands is a highly significant source of variation even though this source can explain only 1.5% of the total variation. Replications accounted for 39% and seedling to seedling variation showed 56% of the total. Stands accounted for 1.8% and probably will prove to be significant even though a specific F test was not possible in this experiment because of the families in stands significance. The interaction components in total show less than 1% of the variation.

When the percent defoliation by stand is ranked (Table 2) an unexpected result is apparent. The stand expected to yield the lowest defoliation gave the highest and the stand expected to give the highest gave the lowest (Table 2).

Table 1.--ANOVA for % western spruce budworm defoliation of Douglas-fir seedlings accounting for both stands and families in stands.

Source	df	MS	EMS	F
Rep	1	74.31	$\sigma^2 + r\sigma_{ac,b}^2 + rc\sigma_{ab}^2 + rcb\sigma_a^2$	
Stand	3	1.96	$\sigma^2 + ra\sigma_{c,b}^2 + rca\sigma_b^2$	6.53 <sup>nt</sup>
Rep x stands	3	.31	$\sigma^2 + r\sigma_{ac,b}^2 + rc\sigma_{ab}^2$	
Fam in stands	24	.30	$\sigma^2 + ra\sigma_{c,b}^2$	3.00***
Rep x fam in stands	24	.13	$\sigma^2 + r\sigma_{ac,b}^2$	
Within fam	2013	.10	$\sigma^2$	

nt = no test

\*\*\* = significant at the .0001 level.

Table 2.--Ranking of stands by % defoliation of Douglas-fir seedlings  
exposed to western spruce budworm.

Stands	Condition	Seedling defoliation
1. Cedar Creek	Survivors	.52
3. Little Goose Creek	Light def*	.49
4. Grave Creek	Survivors	.43
2. Hull Creek	Heavily def	.42

\*Lightly defoliated Douglas-fir in an area of heavily defoliated grand fir.

Table 3.--Ranking of open pollinated families for % defoliation on  
Douglas-fir seedlings exposed to western spruce budworm.

Seed Trees	PD	Seed Trees	PD
14	.62	33	.45
11	.56	27	.44
35	.56	23	.44
13	.53	36	.44
34	.53	47	.43
12	.53	43	.42
32	.53	21	.42
44	.51	46	.41
15	.51	16	.40
17	.50	45	.40
31	.50	24	.38
41	.49	26	.38
25	.47	22	.37
37	.47	42	.35

Table 4.--ANOVA<sup>1</sup> for family heritability analysis of open pollinated progeny from 28 Douglas-fir exposed to western spruce budworm larvae.

Source	d.f.	d.f.	MS	E.M.S. Model II	Variance Components
Reps	r-1	1	73.3	$\sigma_w^2 + n\sigma_{rf}^2 + nf\sigma_r^2$	
Female parent	f-1	27	.43 <sup>2</sup>	$\sigma_w^2 + n\sigma_{rf}^2 + nr\sigma_f^2$	.0041
Error	(f-1)(r-1)	27	.15	$\sigma_w^2 + n\sigma_{rf}^2$	.0015
Seedlings in families	rf(n-1)	2016	.094	$\sigma_w^2$	.094

<sup>1</sup>Arcsine transformation

<sup>2</sup>F significant at .005

$$h^2 = \frac{\sigma_f^2}{\frac{\sigma_w^2}{nr} + \frac{\sigma_{rf}^2}{r} + \sigma_f^2} = .42 \pm .066$$

The family rankings showed considerable variation from .62 defoliation to .35 (Table 3). The analysis for family heritability yielded a value of  $.42 \pm .066$  (Table 4).

### Discussion

The progeny test was obviously successful in that defoliation was measured and significant family differences were observed. Even though we encountered problems in obtaining hibernating larvae for the 1980 test it has already been shown that second instar exposure will work well (McDonald 1982). Since rep 1 of this test was defoliated lightly by larvae fresh from hibernation (.39) and rep 2 was much more heavily defoliated (.63) by older needle mining larvae from a different area and there was little rep x family interaction, we can tentatively conclude that either method of larval introduction should yield an effective test. The better logistics of obtaining needle mining larvae make it the preferred method.

The unexpected absence of a positive relationship between phenotypic appearance and progeny performance argues for a complex interaction between Douglas-fir and western spruce budworm. The interaction could be complicated by nonlinear relationships in defoliation behavior with tree age, mismatches in geographic variation of both budworm and Douglas-fir would destroy the presumed results, or the natural system could be mediated through interaction with predators and/or parasites. Finally, one cannot overlook physical parameters of the sites where the parent trees are located.

But, one must conclude that genetic interaction is playing a role, since a relatively strong family heritability was obtained. The measured heritability would give a genetic gain from selecting the best family (42) of 5% for each cycle of selection.

This result is encouraging enough that larger scale progeny tests should be conducted to determine the broader geographic implications of progeny testing for resistance to budworm and to determine if higher selection differential might not be possible. These new progeny tests should produce materials suitable for long term field testing in areas of high probability of budworm damage such as the cononic infestations in Idaho and Montana. The results from the 1980 progeny test show that sufficient genetic resistance to defoliation by western spruce budworm is present in Montana and Idaho sources of Douglas-fir to fuel a breeding program, but there is likely too little to be of use in extensive stand management approaches.

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Resistance to White Pine Blister Rust in Sugar Pine:  
Research at the Pacific Southwest Forest and Range Experiment Station

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Early research in the California Region on blister rust resistance in sugar pine was conceptually simple and followed traditional approaches. In heavily infected stands, rust-free phenotypes surrounded by cohorts with dozens or hundreds of separate infections implied a genetic cause of resistance and were the source of initial selections. Controlled pollination among these parents in the wild provided full-sib seed for progeny testing, conducted in simply designed field trials. From 1961, new sets of progenies were planted annually, with susceptible controls, on a site in northern California where rust hazard is chronically high and was made acute by the interplanting of native Ribes spp. between blocks of test seedlings. Apart from intensive culture for the first two years to enhance establishment, trees were left to grow--or die from disease. Grafts of selected parents from diverse stands were established in a common garden clone bank adjacent to the progeny tests for further evaluation of their phenotype, and also replicated in an orchard remote from the site for breeding. Financial and logistical constraints, together with the recalcitrant flowering behavior of sugar pine, precluded sophisticated mating designs for estimating heritability and breeding values with precision; seed trees used were those that happened to produce cones most consistently and abundantly. Nor were personnel, funds, or facilities available for more rapid and "efficient" testing by artificial inoculation in nursery or greenhouse environments. This proved to be fortunate. For, while these kinds of tests presently complement the Region's R&D program in an integral and essential way, the ability to observe and document the responses of individual trees and families under field conditions, through time and different growth stages, has provided our best insights to the structure of resistance in this species. Although much remains to be learned, we believe a sound basis exists for implementing an operational program for sustained improvement.

This paper will summarize our experience on the mechanisms and inheritance of resistance, then indicate important gaps in knowledge that point the direction of our research. The following paper will describe in more detail how research results are being implemented in the breeding program.

Major gene resistance (MGR). The most obvious and dramatic mechanism of resistance to blister rust in sugar pine is a hypersensitive reaction controlled by a dominant gene (4). Cells of needle tissues become granular, die, and fill with dark, tannin-like substances, often in advance of invading mycelium. Macroscopically, the symptom usually expresses as a small, necrotic fleck, readily distinguishable from the bright yellow (occasionally red) lesions that develop and continue to enlarge in susceptible genotypes. Subtle variations on this theme are often noted, however. The size of the necrotic lesion varies, as does the amount of mycelium that develops in the mesophyll tissues beneath. Rarely, mycelium is able to penetrate the endodermis and grow down the phloem, but upon reaching bark tissues at the base of the needle fascicle, another hypersensitive reaction is triggered which prevents further spread. Since different sized lesions are frequently seen on the same seedling, the most likely source of this variability is in spore genotypes that vary in aggressiveness or pathogenicity. Yet, overall, the reaction of seedlings with MGR has been surprisingly consistent, considering that the inoculum used came from diverse geographic sources and was applied at very high densities (3,4). Typical basidiospore concentrations, ranging from 200-800 spores/mm<sup>2</sup>, induced lesions so numerous on needles that they soon coalesced and could not be accurately counted, yet resistance was not broken.

Not broken, that is, until confronted with a distinctly new and virulent race. This race was detected at the field test site on known resistant genotypes that had grown without symptoms of rust for up to 14 years, long

after susceptible controls had died of infection. Following an unusually severe epidemic in 1976, these genotypes were observed to have multiple, sporulating infections two years later (1). Seedlings of known resistant genotype inoculated with spores derived from these trees showed uniformly susceptible type reactions in both foliage and bark (2).

The long range value of MGR will depend on the present geographic distribution and frequency of this virulent race, and the speed with which it can spread to new areas. Limited evidence indicates that it may be rare in rust populations. It has only rarely been detected in nursery and greenhouse tests in spite of heterogenous sources of inoculum used in massive doses. Nor was it detected in either of two supplementary field progeny tests, one located only 10 miles east of the site on which it was first detected and the other about 200 miles southwest. In any event, unless and until the virulent race approaches a high frequency regionwide, MGR will provide some protection to artificial regeneration, and we intend to use it fully to this end.

The frequency of the major resistance gene itself is low but variable in natural subpopulations of sugar pine, ranging from nearly nil in parts of the Klamath and Siskiyou Mountains in northern California and Oregon to almost 0.1 in the southern Sierra Nevada. Consequently, it would be difficult to identify adequate numbers of resistant genotypes, for clonal seed orchards in some parts of the range without screening very large numbers of parents. Even if such massive screening were feasible, the parents with resistance might be undesirable by other criteria, such as growth and form. Because the gene is dominant and expresses as early as the cotyledon stage, the problem can be circumvented by screening susceptible parent genotypes for individual seedlings that have captured the resistant gene through open-pollination in wild stands. Rapid screening of large numbers of seedlings per parent is possible in containerized greenhouse tests with minimum space (3). This allows the focus of selection to be placed on desired phenotypic characteristics of the parent other than rust resistance. Resistance will be obtained from an unknown pollen donor, but half of the additive genetic variance of the parent selected for growth and form will also be realized. Seedlings resulting from this selection and screening process can then be grown in production orchards with little compromise in either growth traits or resistance from MGR. The remaining problem to solve is the vulnerability of MGR to the virulent race.

Slow rusting (SR). Sugar pines lacking MGR are highly, though not uniformly, susceptible. Although most seedlings in all families eventually become infected and die within a few years under the stringent field conditions at the test site, they do so at different rates. When measured by the apparent infection rate ( $r$ ), mean values of half-sib progenies from rust-free parents varied continuously over a range from 0.26 to 0.88 after 6 years in the field (1). Full-sib families from specific crosses had a much wider range--from 0.01 to 2.04. For want of a better term, we have adopted the designation "slow rusting" used by cereal breeders to express apparently quantitative differences in susceptibility.

Despite the more than 20 fold range in  $r$  values, levels of SR in trees selected to date are not adequate for use in commercial silviculture without further improvement, since it little matters to the forest manager whether mortality from disease occurs in 2 or 10 years. But the variability observed appears to be additive, and thus amenable to continued improvement. Progeny of relatively slow-rusting parents mated to each other have only half the  $r$  value, on the average, of progeny of the same parents crossed to fast-rusting parents, and only a quarter of the value of progeny from fast x fast parents. If this kind of improvement is sustained, effective resistance might be realized in only two or three generations of selection and breeding.

Nevertheless, infection rate is a crude parameter of resistance. More precise quantitative measures are needed that relate to specific mechanisms of resistance and their inheritance. We have long recognized at least two components of SR--reduced numbers of (normal) infections per tree and increased frequency of aborted cankers per tree--but have been unable to demonstrate them until recently. Multiple infections on small seedlings are difficult to measure, because they soon coalesce, and, in any case, the seedling soon dies. Needed was a means of protecting seedlings until sufficient internodal length on stems and branches had developed to enable quantitative comparisons of numbers of incipient infections (blisters) among individual trees and families. This protection was provided by MGR, until the sudden outbreak of the virulent race. By this time, there were enough trees, all several meters tall, from matings of MGR parents with others lacking this gene, to evaluate quantitative levels of resistance previously masked by MGR. The result, as expected, was a much broader range of variation than available before, which was also more precise and useful. Average numbers of infections per tree (on an equivalent sample of branch internodes) ranged from 1 to 30 among families, and from 0 to over 60 among individual trees. Families from slow-rusting parents (as determined by  $r$ ) averaged only half the numbers of infections of families from fast-rusting parents. Reduced numbers of infections per tree can be taken as an index of low receptivity to infection, a common parameter of resistance in crops, in these genotypes. In pines, this mechanism could operate by preventing establishment of the pathogen in either needles, bark, or both.

Bark reactions, resulting in collapsed, necrotic cankers were another frequently observed resistance mechanism. They signify incompatibility between host and pathogen, and show wide variation in size and shape. The frequency of bark reactions seems to vary among families, and sometimes compatible and incompatible infections exist on the same tree. Rarely, trees without symptoms are found.

We do not understand the inheritance of any of these mechanisms yet. When gross parameters such as percent infection or infection rate are used, the pattern seems additive. But when separate mechanisms are examined, specific host/spore genotype interactions are suggested that may be more simply inherited.

Sugar pine has been long recognized as one of the most susceptible white pines to blister rust, because resistant genotypes are rare. Our experience strongly suggests that adequate numbers of resistance genes to work with exist, but are scattered throughout the population at low frequencies. The problem, simply, is to get these genes together, concentrated into new genotypes.

Ontogenetic resistance. A third kind of resistance is age dependent: certain genotypes are highly resistant as mature trees, yet transmit high susceptibility to their offspring (1). We do not know when this resistance becomes effective, or how it is inherited, but the variation in susceptibility among genotypes is impressive. Mean number of infections per ramet ranged from 0 to over 50 among 60 clones lacking MGR. Seven clones had no infection and 5 averaged over 20 infections per ramet.

Ontogenetic resistance appears to be very strong and stable. When the race virulent to MGR hit in 1976, progenies from MGR parents became infected to varying degrees, some of them heavily. Yet ramets of the same parents in the clone bank adjacent to the progeny tests were little affected. Half of the 18 different clones carrying MGR remained free of rust, while the amount of rust on the rest ranged from only 0.3 to 2.7 infections per ramet. Resistance of this degree would be useful not only in protecting sugar pine

crops over the latter part of a rotation, but also in reducing the amount and variability of inoculum. Nevertheless, the urgency of obtaining durable resistance in early growth stages makes development of ontogenetic resistance a subordinate priority. Because it can mask juvenile susceptibility, it is important to recognize the possibility of ontogenetic resistance when selecting healthy phenotypes in mature stands.

#### Research

Our practical goal is to integrate MGR with SR in all genotypes that go into production seed orchards. To do this most effectively, we must first identify the specific resistance mechanisms, and, if possible, their genetic control. Our approach is to select individuals showing different resistance mechanisms in field tests (such as bark reactions and reduced numbers of infections) and test their progeny by both natural and artificial inoculation. If correlations between the two methods are high, efficiencies realized by nursery or greenhouse tests will accelerate screening of large numbers of candidates.

At the same time, we will place much more emphasis on learning about genetic variability in the rust, especially with respect to pathogenicity. This is an essential complement to knowledge of resistance in the host, as our experience with MGR has shown. Of high priority will be to determine the geographic distribution and frequency of the race virulent to MGR, so that we will better know the present level of protection we can expect from this source of resistance in different areas. It will also give us a baseline to measure how rapidly the frequency of this race is able to increase over time. Nor can we assume that the components of slow rusting are equally effective against all of the extant variability in the rust. If they are not, a series of investigations of host-parasite interaction on a mechanism-by-mechanism, or perhaps gene-for-gene, basis is implied.

Obviously, this could be a long-term venture, but we hope to find some shortcuts. One approach is by getting better genetic control of the rust, through the development of monouredial clones. Such clones, used as sources of inoculum on pine genotypes with different kinds of resistance, should give us a better idea of the range of variability in pathogenicity in the rust population. At the same time, they should also provide more insight into host resistance mechanisms, because of the complementarity that often exists in host-parasite interactions. For example, consistent reactions for a virulence or a low infection type found in certain clones would imply corresponding mechanisms and genes for resistance in the hosts tested.

The point is, that to identify specific genes, genetic control must begin somewhere. With forest trees, both operational and research programs have usually opted for the host, structuring it into family units--most frequently open-pollinated. Usually, heterogeneous and genetically undefined sources of inoculum are used to challenge these. While valid and effective for "picking the winners," i.e., discriminating levels of relative resistance, genetic precision is all but lost. Selfed and full-sib families increase precision, but disadvantages in time and cost of breeding trees, especially pines, needs no elaboration. Although technical difficulties certainly exist in keeping pedigree control of the pathogen, the possibilities of more rapid progress in unraveling host-parasite interactions by this approach are attractive.

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Rust Resistant Sugar Pine (Pinus lambertiana)  
in the  
Pacific Southwest Region

Sugar pine is the largest and most valuable of western pines and is a major component of the Mixed Conifer Forest, generally comprising 5 to 25 percent of the type and occasionally up to 60 percent. It is also a minor component of some ten other forest types (Griffin and Critchfield 1976).

Sugar pine occurs on 2.2 MM acres in California of which 1.5 MM are National Forest. Over one-half of these acres occurs on the Klamath, Shasta-Trinity, and Plumas Forests where blister rust (Cronartium ribicola) is most intense. Sugar pine is ten percent of the net growing stock of conifers on California National Forests.

Abundance of sugar pine has been sharply reduced by selective logging, mortality from blister rust, and limited use and success in planting. Intensive forest management is expected to enhance the relative importance of sugar pine in reforestation.

With medium to long rotations on productive sites sugar pine is the fastest growing conifer. Selected trees at mid-elevation in the northern and central Sierra Nevada Mts. are commonly greater than 30 in. dbh with growth rates of 5 ft<sup>3</sup> per year at only 70 to 80 years old. Old-growth sugar pine produces high quality products and commands premium prices. Young growth values are about equal to ponderosa pine.

Although highly valued by forest managers for its quality wood and rapid growth, sugar pine nursery stock production in Forest Service nurseries has remained low and stable at 600 M to 700 M seedlings per year (3-4 percent of total). Major obstacles to greater production are low initial survival of bareroot stock and subsequent mortality from blister rust, both of which are currently being reduced through cultural and genetic improvement.

This report focuses on development of genetic resistance to blister rust.

#### Project Summary (1957-1975)

Systematic search for rust-free trees in heavily infected stands began in 1957 on the Klamath N.F., where blister rust was first discovered in California 28 years before. During the next decade 170 intensive selections were made on the Klamath, Shasta-Trinity, and Plumas Forests where rust infection was most severe. Only about 30 percent of the selections were seed or pollen producers, a factor which greatly slowed progress.

The first selections were grafted in 1958 and outplanted in 1960 near Happy Camp on the Klamath N.F. This highly hazardous site served as a "disease garden" for evaluating both parent clones and their offspring. A duplicate set of the parent clones were established in a clonal archive at Badger Hill, a low elevation, very low hazard site in the central Sierras, to use for breeding. By 1975, 394 selections had been made and 270 grafted.



Full-sib progenies were outplanted annually at Happy Camp from 1961 through 1975. Because of low flower production, only half of the selected candidates were tested during this period.

Of the 137 phenotypically resistant candidates evaluated, 22 (16%) carried major gene resistance (MGR): two were homozygotes and the rest heterozygotes. Additionally, three candidates were identified that consistently transmitted a relatively high level of partial resistance, or "slow rusting" (SR). The information obtained was critical, but these evaluations were expensive and time consuming: apart from the cost of control breeding, each progeny required from 3 to 5 years, from seed, to evaluate and about 80 square feet of ground at 1' x 2' spacing.

#### RRSP Project Summary (1976-1981)

In 1976, the PSW Region implemented a new and intensive ten-year Master Plan for improvement of Douglas-fir, ponderosa pine, sugar pine, and white fir, in order of priority. A broad genetic base of each species was desired (about 200 selections per breeding zone) for the production seed orchards. This presented a problem for sugar pine. Selection for improved growth without rust resistance would be self-defeating, but intensive selection for rust-free phenotypes is only possible in heavily infected stands, which tend to be concentrated in the northern forests. We also knew that a maximum of 25 percent of the phenotypes so selected would prove to be resistant genotypes. Clearly, a much more

efficient method of screening was needed to arrive at the goal of 800 candidates set. Research at the Institute of Forest Genetics had shown that MGR could be reliably detected by the type of symptom produced on cotyledons after artificially inoculating open-pollinated seedlings with high spore densities. By this means (COT test), 100 seedlings/ft<sup>2</sup> can be inoculated in convenient containers and evaluated for MGR within 3 months of sowing. In the last five years, numbers of MGR genotypes identified has increased from 22 to 138. Because of these economies in time and space, phenotypic selection for rust resistance can be relaxed and refocused on growth and form.

The resulting frequency of resistant parent genotypes identified is only somewhat lower than before but is more than compensated by the ability to detect and recover individual, resistant seedlings among open-pollinated progenies of susceptible genotypes. These seedlings will substitute for their parents in first-stage production orchards; they will combine resistance derived from unknown MGR donors and half of the additive genetic variance of their selected parent for other desirable traits. MGR frequency is quite low in north.

Just when the greenhouse screening work got going, a virulent race to MGR trees was discovered at Happy Camp during the 1978 evaluation following a severe epidemic in 1976. Even though the potential for this virulent race was recognized from the beginning, no mass screening for other resistance types had been initiated because of the uncertainty

of their mechanism, inheritance, and identification. Emergence of the virulent race provided a grand opportunity to examine MGR trees for other resistance mechanisms.

Following the direction established in the Master Plan (1976) using four breed zones (Fig. 1), the effort during this period concentrated on selecting rust-free trees, primarily on the Klamath N.F. (BZ-1), testing them by greenhouse inoculations, and then grafting the proven MGR parents at Chico Tree Improvement Center (CTIC) orchard and at Badger Hill clone bank.

In 1979, 33 clones (30 MGR, 3 SR) were grafted at Chico Tree Improvement Center for the BZ-1 orchard.

Additionally, work in the Sierras (BZ-3, BZ-4) consisted of selecting more intensively for growth and form superiority as well as freedom from rust. In BZ-3, 116 new selections were added to the 284 older rust-free selections. In BZ-4, 172 new selections were made. Most new selections were grafted into the Badger Hill clone bank.

#### RRSP Project Plans (1982+)

The long-range goal is eventual integration of MGR, SR, and superior growth, form, and adaptability into every clone in production seed orchards. Inevitably, this will be a gradual process requiring at least 20 years of selection, testing, breeding, and seed production (see Fig. 2). The degree of improvement in growth traits from progeny tests depends to a large extent on the size of the genetic base of proven resistant stock available for roguing.

The medium-range goal is to produce orchard seed from MGR parents and  $F_1$  progenies combined with some SR progenies from Happy Camp starting in 10 to 12 years. This first-stage orchard seed will have 75% MGR plus some SR increment of resistance.

Meanwhile, a short-term goal of reforestation with planting stock having a relatively high level of resistance (50%) from MGR can be implemented immediately. Nearly 140 MGR parent genotypes, fairly evenly distributed among breed zones (Table 1), have been identified and more will be found over the next 5 years.

Seed for the short-term goal will come from:

- 1) MGR parents in wild stands (wind-pollination)
- 2) MGR parent grafts at Badger Hill (wind-pollination)
- 3) MGR pollen crossed with wild, heavy, cone producers
- 4) MGR pollen crossed with grafted, heavy, cone producers

#### Organization--Staffing--Cooperators

Currently the PSW Region tree improvement personnel consist of five to ten full-time employees at each of three units: Klamath S.O., Eldorado S.O., and Chico TIC. The Klamath and Eldorado units are responsible for selecting trees, collecting scions/seed, and establishing and maintaining the Happy Camp and Badger Hill plantings, respectively. PSW Research at IFG is responsible for greenhouse testing and evaluation of candidates. Chico TIC is responsible for BZ-1 and BZ-3 production seed orchards and for growing

progeny stock. Other sugar pine seed orchards will be developed at Foresthill under the technical direction of the Eldorado unit.

For the next five years the objective is to evaluate 200 families per year for MGR.

Members of the California Tree Improvement Association have expressed interest in cooperating in making selections in the wild and supplying seed for testing. Three members have participated on a small scale thus far.

Over the past five years less than 10 percent of the tree improvement effort has been with sugar pine. As testing, breeding, and seed production accelerates, this effort will more than double.

#### Site Hazard Rating

The PSW Region Forest Pest Management staff has developed simple, general guidelines for site hazard rating and potential management strategies. Three factors are important in rating site hazard:

- 1) sugar pine population density and amount of rust infection on pine,
- 2) Ribes population density and amount of rust infection on Ribes,
- 3) topography (slope position and aspect) of the site.

Using these criteria, sites can be approximately evaluated for rust hazard (Fig. 3). The response to the various levels of rust hazard may vary among Forests depending upon the overall rust hazard on the Forest as a whole. Confidence in hazard rating decreases when hosts are not present on the site. Information can be kept on stand record cards and maps.

Management options are:

- 1) high hazard - plant resistant (MGR & SR) stock or non-host species;
- 2) moderate hazard - a) plant susceptible sugar pine at higher density, b) control Ribes and/or plant MGR stock;
- 3) low hazard - assume damage from rust negligible; use stock most improved for rapid growth.

Sugar pine should be planted in mixture with other species on all sites. Still needed are quantitative estimates of expected mortality of susceptible stock at each hazard level.

#### Seed Production - First Decade (1982-1992)

All stock with 50% MGR must come from: 1) MGR seed trees in wild or clone bank, and 2) susceptible trees in wild or clone bank control-pollinated with MGR pollen.

Currently, excluding the use of MGR pollen on wild trees, the estimated capability for annual production is 500 acres of pure sugar pine plantations or 2500 acres of 20% sugar pine mix, and in five years this would double due to discovery of new MGR trees and increased seed yields in the clone bank. At best this represents only 20% of the desired rust resistant sugar pine reforestation goal. However, this production could again be doubled, if MGR pollen was used to control-pollinate 250 wild, roadside, heavy, cone-producers.

A cost comparison was made between the use of seed from control-pollinated (50% MGR) and wind-pollinated susceptible trees in wild stands (Table 2). The cost per surviving seedling was about equal if the site hazard resulted in 15% mortality of susceptible genotypes in the first decade. At

site hazards of 25% and 50% mortality of susceptibles the control-pollinated stock was 9% and 40% cheaper, respectively, than ordinary susceptible stock (Fig. 4).

By 1985 an estimated 1 MM sugar pine nursery seedlings will be produced for this Region of which about half could come from collecting seed from MGR trees and clone bank. If the remaining 500 M seedlings are susceptible genotypes planted on sites with 50% mortality of susceptibles, a \$250,000 loss would result. But, if these were from control-pollinated seed the loss would be only \$134,000 in rust-caused mortality.

Since the desired level of sugar pine nursery stock production having 50% resistance is 2.5 MM, lower production levels mean losses in future volume and value returns because sugar pine is superior in growth to other species on sugar pine sites.

Another alternative is vegetative propagation of MGR seedlings. Hedging young seedlings for rooted cuttings of short shoots holds promise, but the major drawbacks are high cost and time to generate large quantities of stock. Control-pollinated seed appears the better approach to stock expansion, but will require commitment to field pollination on the District level. Some control-pollination work has already begun on the Six Rivers N.F. and will begin next spring on the Klamath N.F.

#### Seed Production Orchards - Second Decade (1992<sup>+</sup>)

Implementation has begun under the new strategy (Fig. 2). Initial emphasis is on two breed zones (BZ-1, 3) where rust

hazard and stock needs are greatest. These orchards will be established at Chico TIC with planting beginning in 1984 on 14- and 18-acre parcels. The other two breed units will be planted at Foresthill.

The process initiates with 200 or more selections in wild stands. O-P seed from wild parents are tested for MGR in the "COT" test at IFG. MGR seedlings from MGR parents are out-planted at Happy Camp for subsequent screening for slow rusting (SR). Here, the race of race virulent to MGR allows other types of resistance to express. O-P progeny showing both MGR from "COT" test and SR from field test will be grafted into the second stage orchard. MGR seedlings from open-pollination of susceptible seed parents will be planted directly into the first stage orchard together with MGR parents. Grafts from a few  $F_1$  progenies from early tests at Happy Camp will also be included.

From this point on the cycle is repetitive. Starting with the second stage orchard seedlings produced will have 75% resistance from MGR plus useable levels of SR. The first stage orchard will generate seed mainly with MGR (75%) plus some level of SR derived from the grafts of  $F_1$  progenies currently at Happy Camp.

Since selection and flow of new improved material occur in relatively short intervals orchard development must be progressive over the available acreage. For example, first stage orchards could be completed by 1984-85, but second-stage orchards could not begin until 1990 and could not be



completed until 2002. Therefore, the allocation of available space to the various components of improved material will require further consideration.

Progeny testing for growth and form improvement was not shown in Fig. 2, but it will be part of the process. For breed zones where high hazard exists, orchard stock must have resistance and other traits are only secondarily important. Therefore, selection for growth must be within the base of resistant material and the size of this base should be large enough to allow a 50% roguing for growth without adversely affecting the diversity of orchard seed.

In May 1982, 350 grafts were made at Chico TIC from the best  $F_1$  survivors in older plantations at Happy Camp. Although the genetic base is small, these highly resistant trees will represent the important slow rust component of the BZ-1 first stage orchard. MGR parent clones now total 34 with over 300 grafts and more will be added after testing this year. The third component of the BZ-1 first stage orchard will be  $F_1$  seedlings with MGR from pollen and 160 susceptible families will be screened this fall. It is anticipated that at least 100 families will show a few MGR seedlings from pollen and these seedlings will be planted directly in the Chico TIC orchard.

In 10 years the annual orchard production on 14 acres should be 800 M seed which will plant approximately 5000 acres of 20% sugar pine mixture.

Other breed units will be similarly developed with modifications according to specific needs.

Table 1. Distribution of MGR genotypes by breeding and seed zones in Region 5.

<u>Breeding and Seed Zone</u>	<u>No. of Select Candidates</u>
<u>Breeding Zone 1</u>	
301	35
302	1
311	6
321	<u>2</u>
	44
<u>Breeding Zone 2</u>	
(372)	1
<u>Breeding Zone 3</u>	
522	11
523	6
524	22
525	<u>12</u>
	51
<u>Breeding Zone 4</u>	
526	4
531	8
532	3
533	5
534	5
(540)	<u>17</u>
	42
<u>All Zones</u>	138

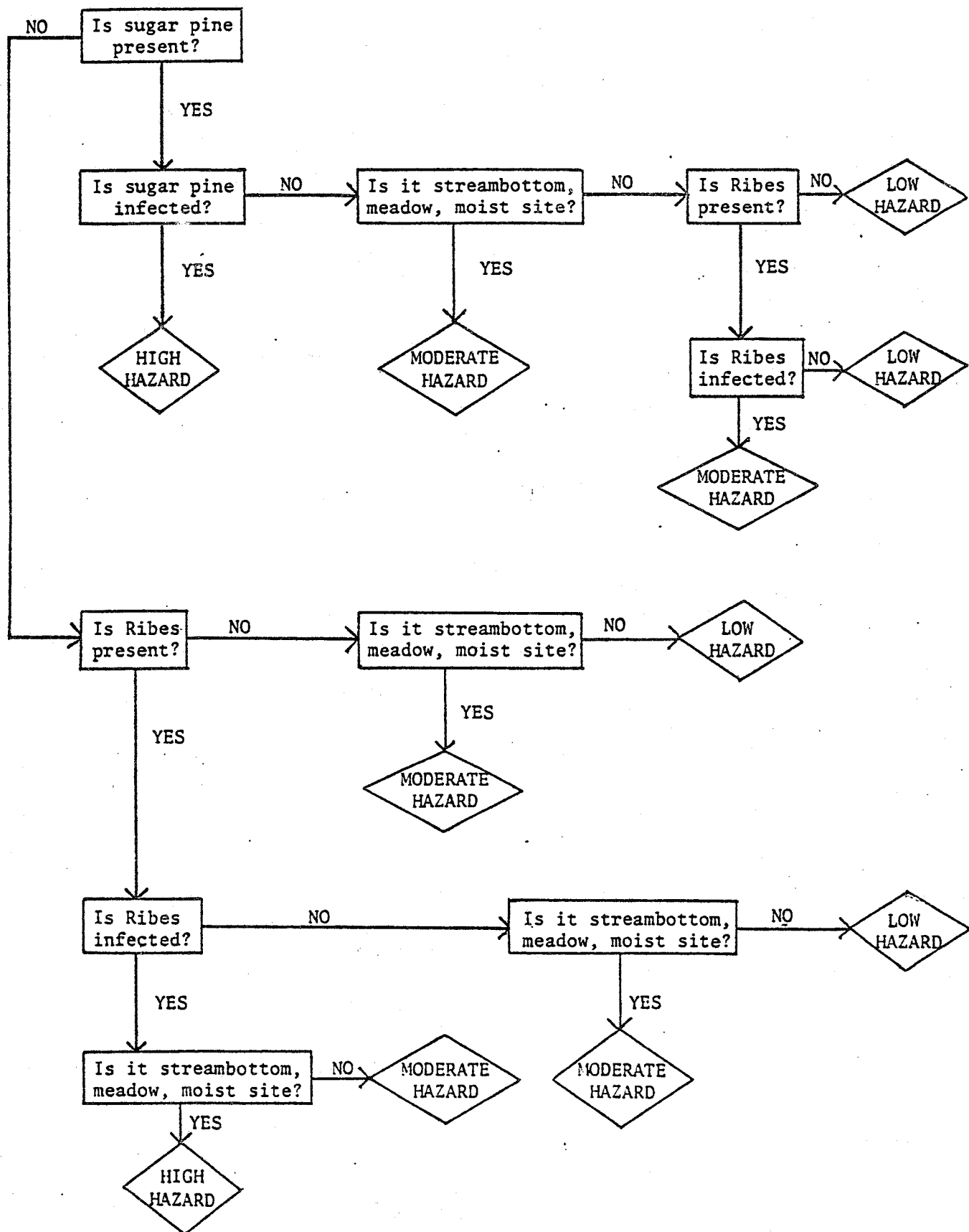
Table 2 . Cost comparison between control-pollinated rust resistant sugar pine seed and wind-pollinated susceptible seed for various site hazards.

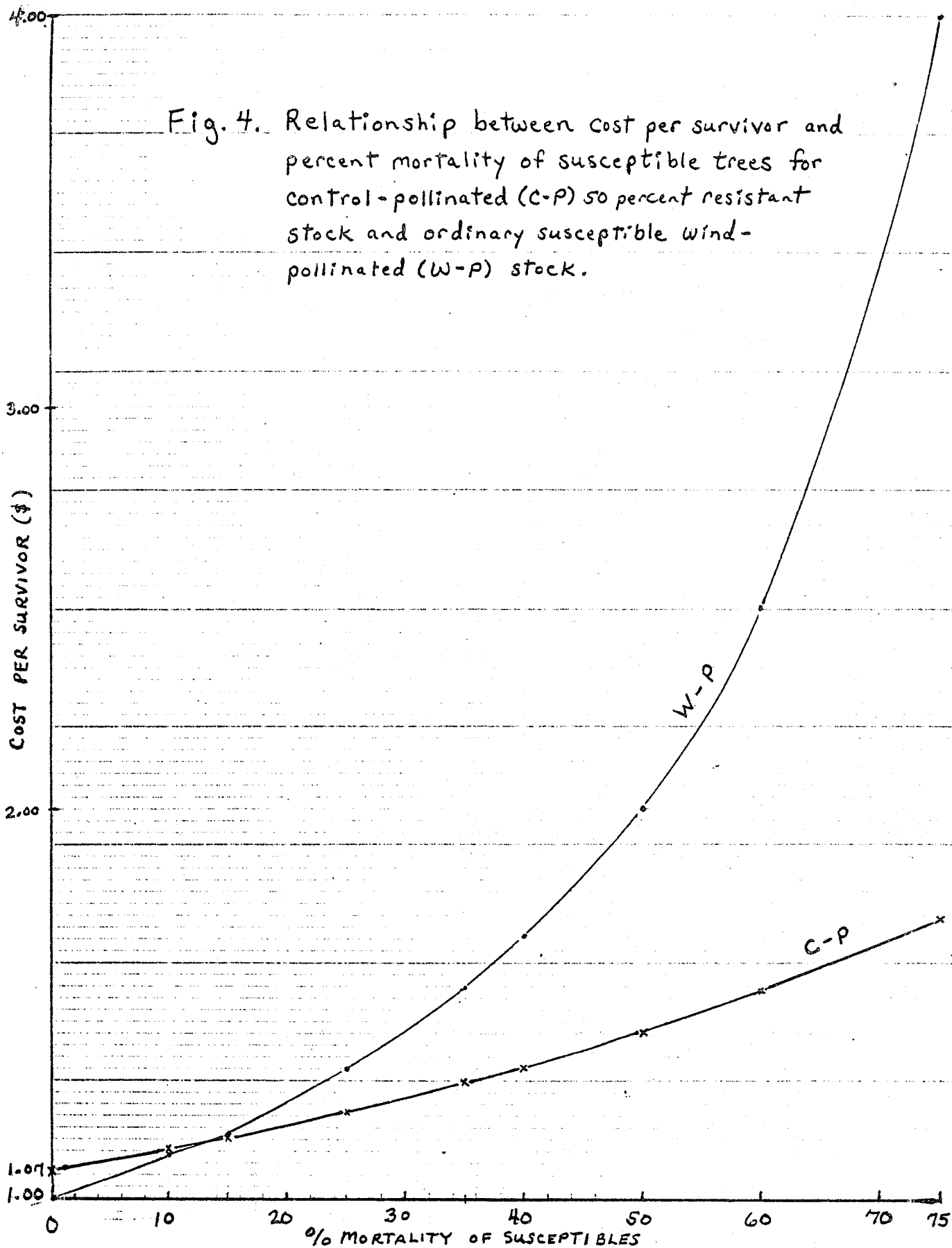
<u>CONTROL-POLLINATED</u>		<u>WIND-POLLINATED</u>
\$150 per tree (Pollinate & Collect)	COLLECT 20 cones 3000 seed	\$40 per tree (Collect Cones)
5¢ per seed	↓	1.33¢ per seed
\$75 per 1500 seed		\$20 per 1500 seed
\$80 fixed nursery cost	2000 seedlings	\$80 fixed nursery cost
\$155 per M seedlings		\$100 per M seedlings
	\$350 per Acre (Site Prep, Plant, Post 5-yr cost)	
\$428 per Acre (0.86 per Tree)	500 Trees/A	\$400 per Acre (0.80 per Tree)
\$1.07 per Survivor	20% General Mortality (400 Survivors)	\$1.00 per Survivor
200 Trees Resistant		0 Trees Resistant
<hr/>		
250 Survivors \$1.712 per "	75% Mortality of Susceptibles	100 Survivors \$4.00 per "
300 Survivors \$1.427 per "	50% Mortality of Susceptibles	200 Survivors \$2.00 per "
350 Survivors \$1.223 per "	25% Mortality of Susceptibles	300 Survivors \$1.333 per "
370 Survivors \$1.157 per "	15% Mortality of Susceptibles	340 Survivors \$1.176 per "
380 Survivors \$1.126 per "	10% Mortality of Susceptibles	360 Survivors \$1.111 per "



YEA







Research on the Genetics of Pest Resistance  
at the Intermountain Forest and Range Experiment Station

by

R. J. Hoff

INT has been involved with rust resistance in western white pine since 1950. We have observed many mechanisms of resistance and have seen several rust races. The resistance types are described in Hoff and McDonald (1980) along with how candidate trees are selected, a description of rust inspection methods, how we observe the mechanisms, and our philosophical base for selecting for natural and artificial seed orchards.

Another paper that will be of interest to some of you is Dick Bingham's (who started breeding for resistance at INT) story of the initial 25-year research and development program. In the northern region it is called phase I. Probably some of the most important items in it are on how decisions are made. We all know that we make good decisions and it is nice to see the results. We also try to forget the bad ones--most of us never do. Whoever makes the decisions must balance conservatism against daring--both have their price.



Briefly, I will now describe the methods and observations involved with the white pine blister rust resistance program.

Inoculation. First two weeks of September after the seedlings have completed their second year's growth, using detached leaves that are suspended over the seedlings. Duration: 3 days at 100 percent humidity and cool temperature (15-20°C).

First Rust Inspection. Timing: 9 months after inoculation. Criteria: count needle spots on secondary needles of each seedling by color type, on uppermost two fascicles and measure length of fascicles. We would like to have an average of 8 spots per lineal meter of needle tissue.

Second Rust Inspection. Timing: 1-year after inoculation. Criteria: presence of needle spots on secondary needles plus stem symptoms. We have seen four symptoms: normal cankers; small circular and shallow necrotic areas of sunken bark around the base of a single needle bundle; shallow to deep necrotic areas in the needle portion of the seedling stem that partially encircle the stem; shallow or deep necrotic areas in the needle portion of the stem that completely encircle the stem. We often see symptoms of a normal canker on the edges of the last two stem symptoms.

Third Fourth, and Fifth Rust Inspections. Timing: two, three, and four years after inoculation. Criteria: presence of stem symptoms as listed above plus health of each seedling.

The mechanisms that we have observed are listed in Table 1.

Table 1.--Observed resistance mechanisms in *Pinus monticola*: *Cronartium ribicola* system

Mechanism of resistance	Resistance type*	Hypothesized inheritance	$h^2$
1. Resistance in secondary needles that prevents spot formation	Vertical	?	
2. Foliage resistance in secondary needles to a yellow-spot forming race	Vertical	Recessive gene	
3. Resistance in secondary needles to a red-spot forming race	Vertical	Dominant	
4. Resistance in secondary needles to a yellow-green-island spot forming race	Vertical	Dominant gene ?	
5. Resistance in secondary needles to a red-green-island spot forming race	Vertical	Dominant gene ?	
6. Reduced frequency of secondary needle infections	Horizontal	Nondominant gene ?	0.37
7. Premature shedding infected secondary needles	Vertical	Recessive gene	
8. Fungicidal reaction in short shoot	Vertical	Recessive gene	
9. Slow fungus growth in secondary needles	Horizontal	Polygenic	.46
10. Fungicidal reaction in stem	Vertical Horizontal?	Oligogenic ?	.367
11. Slow fungus growth in stem	Horizontal	Polygenic ?	0.21-0.46
12. Tolerance to infection	Horizontal	?	
13. Branch cankers with no cankers on main stem	Horizontal	?	

\*There are two major kinds of resistance: those that inhibit infections and those that inhibit growth of the pathogen after infection. The first is called vertical and the second, horizontal.

The first nine factors are located in the secondary leaves. The spot prevention type was added recently based on two separate observations. In the past we have listed trees with no spots as escapes. However, we have never been able to infect more than 99% of the  $F_1$  seedlings. In a comparison of  $F_1$  and  $F_2$ , the needle infection rate was 1% versus 15% (Hoff, McDonald, and Bingham 1973). Also, the highly resistant white pines tested at Moscow had a high percentage of this type (Hoff, Bingham, and McDonald 1980).

The four needle spot color types appear to be a typical gene-for-gene relationship that is so common with agronomic crops. It takes a lot of time to prove these races; i.e., separate them and run them through the system individually, but we are working on it. McDonald will discuss races later on at this meeting. One of the pieces of evidence that we like is the additivity of the spots (Table 2). Simply, if a seedling is susceptible to, say, both red and yellow races, it will, on the average, have twice the number of spots when compared to seedlings that are susceptible to only red or yellow (McDonald and Hoff 1975).

Table 2.--Distribution of average needle-spot class on Pinus monticola seedlings for three combinations of inoculation year and age, 9 months after Cronartium ribicola inoculation

<u>Inoculation</u>		<u>Double-type seedlings</u>					
		Yellow-type	Red-type	Single types			
Year	Age	seedlings	seedlings	Yellow	Red	Combined	combined
1966	2-0	12.11*	9.55	13.11	7.01	20.12	21.66**
1970	2-0	7.66	9.85	6.75	10.47	17.14	17.51
1970	3-0	7.00	9.14	6.91	11.58	18.49	16.14

\*Unweighted means expressed as spots per meter of needle length.

\*\*The mean of the single-type yellow seedlings was added to the mean of the single-type red seedlings.

Within these races we have observed a ten fold difference in the frequency of needle spots. This could be due to something in the plant to make it less susceptible to all races or could just be due to the interaction of more races (Hoff and McDonald 1980).

In June 1967, we chose a sample of families and seedlings within families within three large factorial tests that Bingham had set up. These seedlings had been inoculated in September 1966. We counted needle spots, noted their color and shape, and analyzed the data. Bingham's crew who were cone bagging, collecting pollen, and pollenating in May, June, and July did not do the "main" rust inspection until late August and September of 1967. We compared our means to theirs. We differed by more than 20%. The discrepancy was due to the premature shedding of needles with needle spots (McDonald and Hoff 1970). Observations in subsequent tests showed that needles started to dry up and fall off about the middle of June reach a peak in July and is usually completed the first part of September.

The reaction that we call fungicidal reaction in short shoot was found in those seedlings that had needle spots, didn't shed their needles by September, and didn't show up with a stem symptom. The reaction appears to be initiated after the fungus has grown down the needle and into the short shoot (Hoff and McDonald 1971). Since the short shoot is actually stem tissue, maybe this reaction should be considered to be a bark reaction type.

The speed of stem symptom appearance; i.e., slow fungus growth in secondary needles, is derived by the ratio of stem symptoms appearance 1 year/4 years after inoculation.

Resistant stem reactions occur at different intensities from a small necrotic area at the base of a leaf to very large areas after girdling the stem. Also, the fungicidal short shoot reaction discussed above may be better classed as a bark reaction. We see two phases of these reactions; one is a necrotic phase that kills host cells in the infected area. Whatever is causing the death of the host cells doesn't have a lot of direct effect on fungus cells. Fairly normal looking fungus cells can still be observed within the necrotic area. The second phase is the typical wound-periderm formation around the necrotic area; i.e., wound. The effectiveness of the bark reactions for various individuals seems to vary in respect to these two phases. At times we have observed large cankers with most of the fungus dead except for a piece here or there. Sometimes the fungus ends up girdling the tree and killing it; other times the fungus succumbs. And there are cases where the fungus and tree are still coexisting after nearly 30 years--starting when the tree was just 3-4 years old (Tables 3 and 4).

A very small percentage (1-2%) of the full-sib progeny that are inoculated at 2 years old express the trait we call slow canker growth (Table 3). The field plantings of the 1952, '53, '54, and '55 progeny tests that Bingham installed are nearly 50 feet tall (Table 4). From 1957 to 1960 Dick's crew moved nearly all the "resistant trees" to a breeding arboretum leaving only cankered trees. In 1981 there were still 214 trees on the plot, 58 of those had large basal cankers out of 4,835 trees that were inoculated (Table 3).

Table 3.--Number of trees with basal cankers; number of trees on the plot, fall 1981; and number of trees inoculated and planted

Progeny test year	Total trees planted #	Trees on plot Fall '81 #	Trees with basal cankers #	Trees with basal cankers %
52	2324	24	11	0.5
54	953	26	12	1.3
55	1558	164	35	2.3
Total	4835	58	214	1.2

Table 4.--Height, DBH, and percentage of circumference of basal canker

Progeny test year	Trees w/o basal cankers		Trees with basal cankers		
	Height	Diameter	Height	Diameter	circum. of canker
	ft	in.	ft	in.	%
52	46	7	44	9	59
54	47	7	47	8	57
55	37	7	36	5	50
X	43	7	42	7	55



I have listed two more "resistance types", but we don't know much about them. Tolerance is a condition of an individual plant that permits it to grow at least fairly normally even though it is infected more or less at the same level as a susceptible plant. We haven't seen any cases where a badly infected tree has lived through a rotation. But we have seen many individual seedlings, and older trees too, that take an awfully long time to die and, until the last couple of years, before the trees die they grow as well as uninfected trees.

Also, we have seen several cases of trees that had only branch cankers. Several forest managers have also brought this to our attention. These could be due to slow canker growth. The fungus just can't get to the bole before the branch flags.

Tables 5 and 6 show the levels of resistance attained for some of the resistance types (Hoff, Bingham, and McDonald 1973).

Table 5.--The level and the mechanisms of resistance of Pinus monticola and P. strobus to white pine blister rust 2½ years after inoculation

Species	Type of parentage	Lots of crosses	Total seedlings	Seedlings uninfected	Mechanisms of resistance					Killed by blister rust
					Seedlings with no spots nor stem symptoms	Premature shedding of infected needles	Fungicidal short shoot	Bark reaction		
		No.	No.	----- Percent -----						
P. monticola	Susceptible	6	546	23.0	4.2	14.5	2.0	2.4	17.8	
	F <sub>1</sub>	10	2,876	41.8	1.2	19.9	5.2	7.7	13.8	
	F <sub>2</sub>	32	3,061	81.8	15.1	47.4	11.5	6.9	7.0	
P. strobus	P <sub>s</sub>	1	99	5.0	0	3.0	0	2.0	79.8	

Table 6.--Resistance and realized gain in resistance to white pine  
blister rust in various lots and/or crosses in *Pinus monticola*

Resistance category	Resistance			Realized gain	
	Susceptible lots	F <sub>1</sub>	F <sub>2</sub>	From susceptible to F <sub>1</sub>	From F <sub>1</sub> to F <sub>2</sub> generation
	----- Percent -----				
Total seedlings uninfected	23.0	41.8	81.8	18.8	40.0
MECHANISMS OF RESISTANCE					
No spots	4.2	1.2	15.1	-3.0	13.9
Premature shedding <sup>1</sup>	14.5	19.9	47.4	5.4	27.5
Fungicidal short shoot <sup>1</sup>	2.4	6.5	21.9	4.1	15.4
Bark <sup>1</sup> Reaction	2.9	10.3	16.8	7.4	6.5

<sup>1</sup>Corrected for the number of resistant seedlings due to the previous mechanism(s) of resistance.

Another publication that I want to bring to your attention is a computer based model of white blister rust (McDonald, Hoff, and Wykoff 1981). This is probably as good a model as can be found with a forest disease today. Geral really did most of it and should be patted on the back for his effort. Also, the blister rust control organization that tried so hard to eradicate the fungus by pulling Ribes and spraying fungicide should be given a lot of praise for their data collection effort. Without their data this model would never have been possible.

This model will help us to predict how the various resistant types will perform in nature. It will help us to align levels of resistance to the amount of rust hazard and it will help us predict how various natural regenerated stands will perform. A lot of natural regeneration is taking place and a common question by managers is "what should I do with all this white pine?" Enough said about hazard determination now. Geral will talk about it later in this meeting.

The first blister rust races that we observed were displayed as differences in color of needle spots. Later on several other races have become evident (Table 7).

Table 7.--Evidence of genetic variation in the western white pine-  
blister rust system

- 
1. Yellow needle spots--normal size, normal virulence
  2. Yellow needle spots--normal size, high virulence
  3. Yellow needle spots--small size
  4. Red needle spots--normal size, normal virulence
  5. Red needle spots--normal size, high virulence
  6. Red needle spots--small size
  7. Yellow island spots
  8. Red island spots
  9. A normal canker and typical resistant bark reaction on the same seedling
-

Geral will also discuss blister rust races later in this meeting so I will say no more.

#### Research on pests other than blister rust

Pest problems are, and will always cause, problems in forestry, especially with intensive management. It is imperative that we recognize that a disturbance of the resistance-susceptibility balance to various pests could--and very likely will-- cause a shift in damage level. In most cases a special breeding program is not necessary to maintain a sufficient balance. But what is needed is a knowledge base that will help us to design evaluation trials that include exposure to various pests. This knowledge will also provide data to predict problems.

Pest problems that we have, or are presently working on:

Spruce budworm--Douglas-fir

Rhabdocline--Douglas-fir

Western gall rust--lodgepole pine

Western gall rust--ponderosa pine

Larch casebearer--western larch

White pine needle blight--western white pine

Root rots--all species

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THE RUST RESISTANCE BREEDING PROGRAM  
IN REGION ONE

By Gerald C. Franc <sup>1/</sup>

I. The White Pine Resource. Western white pine reaches its greatest development in the Inland Empire region of north Idaho, western Montana, and eastern Washington where there are almost 3 million acres of white pine habitat type. Western white pine is one of the most sought after conifer tree species in the western United States. White pine lumber is soft, white, and easily worked, making it useful for a wide variety of wood products. The species reproduces readily, grows rapidly and is generally easy to manage.

The bid rates for 25 timber sales on the Clearwater National Forest during Fiscal Year 1980 were analyzed. The bid price for white pine ranged from \$3 per thousand to \$323 per thousand board feet. The median bid price was \$60 per thousand. The weighted average bid price was \$113.15 per thousand board feet.

During the same period the weighted bid prices for grand fir and Douglas-fir were \$28.01 and \$11.86 respectively. The low bid price for Douglas-fir is the result of low volumes which frequently result in that species being sold at base rates.

A recent issue of the Journal of Forestry showed that the highest bid price for any species in Region One during 1979 was a bid of \$186.00 per thousand for western white pine.

Cooperators in the white pine tree improvement program project an annual need of 4.5 million white pine seedlings for artificial reforestation. The Forest Service accounts for almost one half of the annual needs.

II. Program Objectives. Encouraged by the findings of the research phase of the white pine tree improvement program, the operational white pine program, called Phase II, was begun in 1967. The objectives of the Phase II program are to expand the resistance breeding base by selecting additional rust free trees and to incorporate selection for growth characteristics as well as resistance.

III. Organization. From 1967 to 1975 the program was administered by the Regional Silviculturist and the Forest Silviculturist on each of the "white pine" forests of the Region with Technical Direction from the Intermountain Station at Moscow. In 1975, the White Pine Tree Improvement Program became a part of the Inland Empire Tree Improvement Cooperative. There are presently eleven members of the Co-op participating in the white pine program. Technical direction for the program still comes from the Intermountain Station and the Forest Service. A species director is appointed by the cooperative to coordinate activities.

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<sup>1/</sup> Selective Breeding Specialist, Region One

In addition to the Forest Service and the Intermountain Station, cooperators in the white pine program include Potlatch Corporation, the Idaho Department of Lands, St. Regis Paper Company, Idaho Pine Timber Associates, the Coeur d'Alene Tribe, the University of Idaho, the Port Blakely Mill Company, Diamond International and BN Timberlands.

The cooperators meet periodically to review the program and to develop work schedules. The cooperative effort is guided by the white pine tree improvement plan and work is coordinated through the preparation and use of a biennial cooperative work schedule. The schedule is revised every year.

IV. The Selection of Candidate Trees. From 1967 to 1969, over 3,000 rust free candidate trees were located. Trees were selected for growth and form as well as for the absence of rust infection. Provisions were made for the selection of diseased trees in areas of high infection if the candidate tree had significantly less infection. The average number of cankers per tree in the stand determined how many cankers would be permitted on the candidate. In actual practice, very few diseased trees were selected.

The geographic boundaries and elevational zones established for the research program were followed in making the Phase II selections. Fortunately, each candidate tree has a unique number so that changes in seed zones can be made without complications.

The candidate trees were tagged, mapped, and data collected on tree measurements and site descriptions. A few replacement selections were made in subsequent years.

V. Seed Collection. Cone collections from the new candidate trees began in 1970. Controlled pollinations were made using a 10-tree pollen tester mix from proven Phase I trees. Because of financial limitations and a cone crop failure in 1971, progress towards completing the collections was very slow. In 1974, a decision was made to expedite collections by utilizing open pollinated rather than controlled pollinated cones. The reduced genetic control using half-sib progeny was offset, to some extent, by including more progeny in each test cycle.

The initial cone collection from all 3098 candidate trees was completed in 1981. Some recollection will be necessary for a few families that are to be retested. An inventory of seed will be maintained for each family for the duration of the testing of Phase II material. About 400 trees have been dropped for a variety of reasons including dead, lost and sub-standard.

VI. Progeny Testing. With so many candidate trees in the program, there will be five test cycles. Testing families for blister rust resistance takes place at the Coeur d'Alene Nursery. The first test cycle was inoculated in 1977. Cycle 2 and 3 were inoculated in 1978 and 1981 respectively. Cycle 4 and 5 are scheduled to be inoculated in 1983 and 1985.

Seedlings for rust testing are greenhouse grown and are 2 years old at the time of inoculation. An inoculation chamber is improvised by covering a lath house with canvas and plastic. Mist nozzels and sprinklers are used to maintain the humidity and temperature at as close to 100% and 70° as possible. Infected Ribes leaves are collected from a number of sites around north Idaho just prior to the inoculation. These leaves are suspended 18 inches above the tops of the seedling on chicken wire racks. The racks are rotated around the chamber at regular intervals so that an even inoculation is attained. Spores are collected on microscope slides and spore cast is monitored by staining and counting spores at regular intervals. Following the inoculation, the seedlings are transplanted to nursery beds. The seedlings are planted in the beds in family blocks at a 4x4 inch spacing.

Rust inspections are made in June and September of the first year following inoculation and again in September of the third year after inoculation. The rust screening is designed to rank families for needle lesion frequency and slow canker development and to identify individuals within high ranking families that exhibit no spot, needle shed, fungicidal shoot and bark reaction resistance.

A separate early growth selection trial is established for each test cycle at the Lone Mountain Tree Improvement Area. These seedlings are not inoculated, but are planted at one foot spacing and are provided intensive care. The seedlings in the early growth selection trial are measured at the end of the third growing season concurrent with the final rust inspection. The height data is used to rank families for growth.

For each cycle of testing, a field test is also established. The objective of the field test is to measure family performance for rust resistance and growth under natural conditions. These plantations will provide a long-term evaluation of family performance and allow for the correction of any errors made in the rust selection or early growth trials.

VII. Data Handling and Analysis. Data sets for tree and seed inventory, inspections, test plantations and seed orchards are entered and corrected by the Co-op Data Management Technician. The Forest Service Tree Improvement Technician also helps with data management. Data analysis is provided by geneticists at the Intermountain Station. Data is entered and stored in the Washington State University computer.

VIII. Seed Orchard Establishment. Of significance was the finding by research of very little geographic or elevational variation in western white pine. So strong is the data that it has been possible to eliminate all seed zones for white pine. As a result only one white pine seed orchard is being established by the Forest Service.

At the completion of the third rust inspection for each test cycle, selected individuals from those families ranking high in low needle lesion frequency, slow canker development and height growth are lifted from the transplant beds at the nursery and planted at the white pine seed orchard site at Lone Mountain.

Individuals are selected for the following characteristics:

1. no spots resistance
2. needle shed resistance
3. fungicidal shoot resistance
4. bark reaction resistance

In addition, the individuals must be of average or better growth when compared with other individuals in the family block.

There will be about 4 acres of seed orchard established from each cycle of testing. Selected seedlings identified as having a particular resistance mechanism will be planted together in a group so that interbreeding within the group will increase the gain for that particular mechanism. Resistance groups will be planted adjacent to one another with no attempt to minimize interbreeding between groups and seed from the orchard will be bulked.

The first select Phase II material from test cycles 1 and 2 was transplanted to the seed orchard site in March of 1982. In addition to the Forest Service seed orchard at Lone Mountain, five seed orchards were established by white pine cooperators from the cycle 1 and 2 material.

IX. Natural Seed Production Areas. Another less publicized part of the White Pine Tree Improvement Program is the development of natural seed production areas. This part of the program is designed to take advantage of natural selection. In high hazard areas of mature white pine where rust mortality has been high, the site is prepared and natural regeneration is established from the surviving white pine. Rust selection is allowed to continue in the regeneration and may even be enhanced by planting Ribes bushes on the site.

Eventually the survivors will be rogued and managed as a seed production area. Seedlings produced from the areas will be as much as 40% resistant to blister rust and will be well adapted to natural sites by virtue of their having come from a white pine site.

Three natural seed production areas have been developed and several more are under consideration. One site is just reaching flowering age and has been partially rogued.

X. Utilization of Improved Seed. The availability of improved white pine seed has been a limiting factor in white pine management in Region One. There are presently only two producing white pine seed orchards; one is the breeding arboretum at Moscow and one is the grafted seed orchard at Sandpoint. Three more seedling seed orchards have been established and are just becoming productive. One is at Coeur d'Alene and two are at Lone Mountain. Additional seed orchards are being established as part of the Phase II white pine program.

Meanwhile, seed from other sources are approved for use by Region One Forests as available. Seed sources by priority are:

1. established Phase I and Phase II Seed Orchards

2. Phase I and Phase II white pine test plantations
3. required white pine seed production areas
4. excess white pine tree improvement seed
5. selected unproven white pine candidate trees

At the present time, seed in quantities necessary for operational planting are available only from priorities 1, 4, and 5. The two producing Phase I seed orchards have yielded over 1350 pounds of genetically improved seed since 1970. However, seed from the Moscow Arboretum is shared with other State, private and Federal cooperators in the white pine tree improvement program.

Presently, the higher priority seed sources are used first and the lower priority sources only when higher priority sources are not available. Because of the increased demand for white pine seed all sources are utilized. As hazard mapping techniques are developed the less resistant seed sources will be matched with the less hazardous sites. This will be an interim procedure pending the availability of genetically improved seed from the Phase II seed orchards.

In view of silvicultural and blister rust considerations, the following recommendations are made regarding the planting of western white pine in Region One:

1. Avoid pure white pine plantations. Always include at least one other species in the plantation.
2. Plant those plantations that include white pine at closer spacing than might otherwise be used. This will allow some flexibility in dealing with blister rust silviculturally.

XI. Advanced Generation Selection. Advanced generation seed orchards are planned utilizing grafts from outstanding individuals from the various Phase I test plantations some of which are 25 years old. This material will be incorporated into the Phase II seed orchard being developed at Lone Mountain. The same procedure will be followed in Phase II test plantations and seed orchards as long term data on resistance and growth performance become available.

XII. Research Needs. The following have been identified as high priority research needs in the white pine program:

1. The inheritance and mode of operation of the bark reaction resistance type.
2. The inheritance and mode of operation of tolerance and slow canker growth.
3. The effectiveness of the resistance factors individually or in combination. Can they be bypassed and if so, under what circumstances?

4. Genetic and geographic variation in rust and its effect on the single gene resistance factors.
5. The utilization and usefulness of the low spore production uniform resistance mechanism.
6. The correlation between resistance factors and growth traits.

Also of interest, but of lower priority are:

1. Selection pressure on and resistance in the alternate host.
2. The effect of age and environment on resistance.
3. The development of a remnant stand seed production area to provide a base line for measuring resistance gain and to preserve putative white pine types.

THE WHITE PINE BLISTER RUST PROGRAM

PACIFIC NORTHWEST REGION  
U.S. FOREST SERVICE

by  
SAFIYA A. SAMMAN

JULY, 1982

THE WHITE PINE BLISTER RUST  
PROGRAM OF REGION 6

INTRODUCTION

The objective of this paper is to present an overview of Region 6's white pine blister rust program including background information, present status and future direction.

The western white pine Pinus monticola is one of the valuable conifers native to the western United States. Its range in the Pacific Northwest extends from British Columbia southward to the California border. It is prized for its cleanboled form, soft, white easily machined lumber. It has the ability to reproduce itself naturally and is characterized by relatively rapid and long-continued growth. Its ability to inhabit sites often not favorable for other commercial conifers makes it highly desirable for use by forest managers throughout the species range (Bighan, 1974; Aghanbook 1965). In the Pacific Northwest, western white pine never exists as a pure stand over extensive areas but is a component species of 15 forest cover types in its range. It is associated with species such as Douglas-fir, Grand fir, Western hemlock, Engelmann spruce and other pines at elevations from 1000 to 7000 feet. However, since the introduction of white pine blister rust (Cronartium ribicola J.C. Fischer and Rabenh.) early in the century, it spread epidemically on white pines. In spite of attempts by federal and state agencies to control the spread of blister rust fungus, it has spread throughout the range of the white pines and has had a devastating effect on the species. The regeneration of this species has been severely curtailed in many areas of its range.

In 1956, Region 6 initiated a white pine breeding program. The objective of the blister rust resistance program since 1970 has been to produce



rust resistant strains of white pines and maintain desirable traits such as high wood quality and fast growth typical of the white pines. Multi-factor lines are being developed which make maximum use of horizontal and vertical resistance mechanism defines for the western white pine Blister Rust System. The R-6 breeding program includes three elements:

1. The nursery testing which provides primarily data on rust resistance.
2. A plan to match the resistant level of the plant material available to the degree of blister rust hazard on forest land and for making seed allocations for more efficient use of available seed.
3. Evaluation plantations for high priority breeding zones mainly for growth and form, but also to compare rust resistance results of nursery to field test.

The white pine rust resistance program serve approximately 701,600 acres of R-6 commercial Forest land, which is a small fraction of the R-6 forest land under intensive management. However, the high demand of the species for high elevation sites, where frost is persistent 3/4 of the year and in areas where root rot is prevalent, justifies the breeding program for rust resistant white pines. It is also the best growing species in these high elevation sites. On the Fremont National Forest, white pine is the best growing species with best form. In a plantation on the Mt. Hood National Forest, white pine has outgrown all associated species.

Sixteen of the 19 National Forests in the region are involved in the white pine blister rust program. Tables 1, 2 and 3 shows the distribution of work load by forest for commercial forest land that supports western

Table 1. Western White Pine Breeding Zone Statistics

FOREST	NUMBER OF BREEDING ZONES	ELEVATION (M FT)	COMERCIAL FOREST LAND		POTENTIAL GROWTH FT <sup>3</sup> /ACRE/YR.	ACRES PLANTED/ DECADE	LBS. SEED NEEDED/ DECADE	SELECTED TREE GOAL	IMPROVEMENT LEVEL	SEED ORCHARD ACRES		EVALUATION PLANTATION		PROGRAM PRIORITY	
			OWNERSHIP	M ACRES						TESTED	UNTESTED	NO.	ACRES	FOREST	REGION
Colville	4	2 - 6	NFS 21	22.8		2530	110	200	3	28	0				
Deschutes	3	4 - 7	NFS 01	14	53	2400	103	150	1	0	0				
Fremont	4	5 - 8	NFS 02	4.1	73 - 89	458	206	235	3	37	0				
Gifford Pinchot	3	2 - 5	NFS 03	73.6		6620	254	600	3	30	0				
Malheur	3	4 - 7	NFS 04		40	1600	80	150	1	0	0				
Mt Baker - Snoqualmie	3	1 - 5	NFS 05	131	143	18946	298	138 <sup>a</sup>	3	19.5	0				
Mt Hood	3	2 - 5	NFS 06	38.3	100	3970	235	225	3	8	0				
Ochoco	No Western	White Pine													
Okanogan	3	2 - 5	NFS 08	19	60 - 80	320	16	75	1	0	0				
Olympic	2	2 - 4	NFS 09			1560	78	100	3	7					
Rogue River	6	2 - 6	NFS 10	16.8	80 - 105	2220	161	482	3	22	0	9	63		
Siskiyou	4	2 - 6	NFS 11	17		46	23	189	1	0	0				
Siuslaw	No Western	White Pine													
Umatilla															
Umpqua	4	2 - 6	NFS 15	37	110 - 80	4110	172	335	3	33		12	80		
Walla Walla - Whitman	Figures are not available														
Wenatchee	2	3 - 5	NFS 17	36	101	3000	180	279	3	0 <sup>g</sup>	0				
Willamette	4	2 - 6	NFS 18	69.7	229 - 173	10820	470	550	3	28	0	12	102		
Winema	3	4 - 6	NFS 20	17.8	50 - 80	1020	61	150	0	2	14				
TOTAL				612.2		54607	2217			179.5		35	259		

Table 2. Sugar Pine Breeding Zone Statistics

FOREST	NUMBER OF BREEDING ZONES	ELEVATION (M FT)	COMERCIAL FOREST LAND		POTENTIAL GROWTH FT <sup>3</sup> /ACRE/YR.	ACRES PLANTED/ DECADE	LBS. SEED NEEDED/ DECADE	SELECTED TREE GOAL	IMPROVEMENT LEVEL	SEED ORCHARD ACRES		EVALUATION PLANTATION		PROGRAM PRIORITY	
			OWNERSHIP	M ACRES						TESTED	UNTESTED	NO.	ACRES	FOREST	REGION
Colville															
Deschutes	2	4 - 6	NFS 01	8	55	900	435	100	1	0	0				
Fremont	4	5 - 7	NFS 02	3.5	52 + 73	1626	1155	165	2	0	19	1	7		
Gifford Pinchot	No Sugar Pine														
Malheur	No Sugar Pine														
Mt Baker - Snoqualmie	No Sugar Pine														
Mt Hood	No Sugar Pine														
Ochoco	No Sugar Pine														
Okanogan	No Sugar Pine														
Olympic	No Sugar Pine														
Rogue River	7	2 - 5	NFS 10	12.2	70 - 105	1590	1687	1327	3	33	0				
Siskiyou	6	0 - 6	NFS 11	92.8	101	6883	3438	288	3	43	0				
Siuslaw	No Sugar Pine														
Umatilla	No Sugar Pine														
Umpqua	3	2 - 5	NFS 15	30	85 - 105	3480	935	264	3	33	0	9	60		
Wallowa - Whitman	No Sugar Pine														
Wenatchee	No Sugar Pine														
Willamette	2	1 - 3	NFS 18	5.6	136	1200	600	100	3	14	0				
Winema	5	4 - 7	NFS 20	10.5	52	300	230	50	3	1	7				
TOTAL				162.6		14653	7551								

Table 3. Lodgepole Pine Breeding Zone Statistics

FOREST	NUMBER OF BREEDING ZONES	ELEVATION (M FT)	COMERCIAL FOREST LAND		POTENTIAL GROWTH <sup>3</sup> /ACRE/YR.	ACRES PLANTED/ DECADE	LBS. SEED NEEDED/ DECADE	SELECTED TREE GOAL	IMPROVEMENT LEVEL	SEED ORCHARD ACRES		EVALUATION PLANTATION		PROGRAM PRIORITY	
			OWNERSHIP	M ACRES						TESTED	UNTESTED	NO.	ACRES	FOREST	REGION
Colville	8	4 - 7	NFS 21	143	37 - 145	54400	647	1054		7	24	7	66.5		
Deschutes				382											
Fremont	9	5 - 7	NFS 02	188			523	1000		136	38	24	230		
Gifford Pinchot	No Lodgepole Pine														
Malheur	15	3.5-7.5	NFS 04	94.5	30 - 65	11180	131.6	472	1	0	0				
Mt Baker - Snoqualmie	No Lodgepole Pine														
Mt Hood	No Lodgepole Pine														
Ochocco	4	4 - 6	NFS 07	19.0	50	1260	15	180	1	0	0				
Okanogan	No Lodgepole Pine														
Olympic	No Lodgepole Pine														
Rogue River	No Lodgepole Pine														
Siskiyou	No Lodgepole Pine														
Siuslaw	No Lodgepole Pine														
Umatilla	15	3.5-5.5	NFS 14	207.8		24518	299	490	1 & 2	0	21				
Umpqua	4	3.5-6.5	NFS 15	6.4	59	700	18	200	1	0	0				
Wallowa-Whitman	15	3.5-7.5	NFS 16	90.3	49	5000	143	840	1	0	0				
Wenatchee	No Lodgepole Pine														
Willamette	No Lodgepole Pine														
Winema	13	4 - 7	NFS 20	285.1	35 - 59	30250	626	1825	1, 2, 3	61	42.5	17	221		
TOTAL				1085						68	87.5				

white, sugar and lodgepole pine respectively. Some definitions are needed at this point to clarify a couple of terms used in Region 6.

Breeding Block: A breeding block is a geographic area which envelopes a number of breeding zones. It is delineated on basis of similarities in environmental and ecological factors. For white pine, Region 6 is divided into 18 different breeding blocks (Appendix B exhibit 1).

Breeding Zone: A breeding zone identifies an area within a breeding block in which an improved population of a species will be developed for reforestation. For white pine and sugar pine each breeding block is divided into breeding zones on basis of elevation. Table 4 designated the distribution of breeding zones and code for elevation within the breeding block.

Table 4. Breeding Zone designation for Western White Pine and Sugar Pine in Region 6.

ELEVATION RANGE (feet)	CODE <sup>1/</sup>
0 - 1000	1
1001 - 2000	2
2001 - 3000	3
3001 - 4000	4
4001 - 5000	5
5001 - 6000	6
6001 - 7000	7

<sup>1/</sup> The code of an elevational band always appears in a tree number as does a code for National Forest and breeding block.

#### Improvement Levels Of The Genetic Program

There are three levels of utilizing genetic variation within a species. The Forest Service R-6 sets its goals and priorities based on three levels

of programs intensity. Each level summarizes the intensity of utilizing genetic variation within a species. Different selection and testing intensities are used in these levels. There are three program levels within the Region.

1. Extensive (Low level) program.

The goal of this level is to maintain a large gene pool base and supply source identified seed for reforestation purposes.

2. Intermediate (Mid level) program.

The purpose of this level is to maintain a broad genetic base and supply seed from untested seed orchards.

3. Intensive (High level) program.

The goal of this level is to maintain a broad genetic base and supply tested seed with disease resistance for reforestation purposes.

Figures 1-3 illustrate the level of activities in the three program intensities.

#### Organization Staffing

Overall guidance for the tree improvement Forest Genetics Program for the National Forests in the Pacific Northwest Region is the responsibility of the Regional Forester and Regional Geneticist. Regional plans/goals and technical direction is provided by the Regional office (FSM 2475.11).

Due to the high complexity and high technical competence needed to meet the objective of the blister rust resistance program, the Regional Forester decided to centralize the program at the Dorena Tree Improvement Center to insure high quality and long range continuity. The program geneticist is responsible for providing direction and technical guidance to Forest and District personnel who are responsible for implementing approved

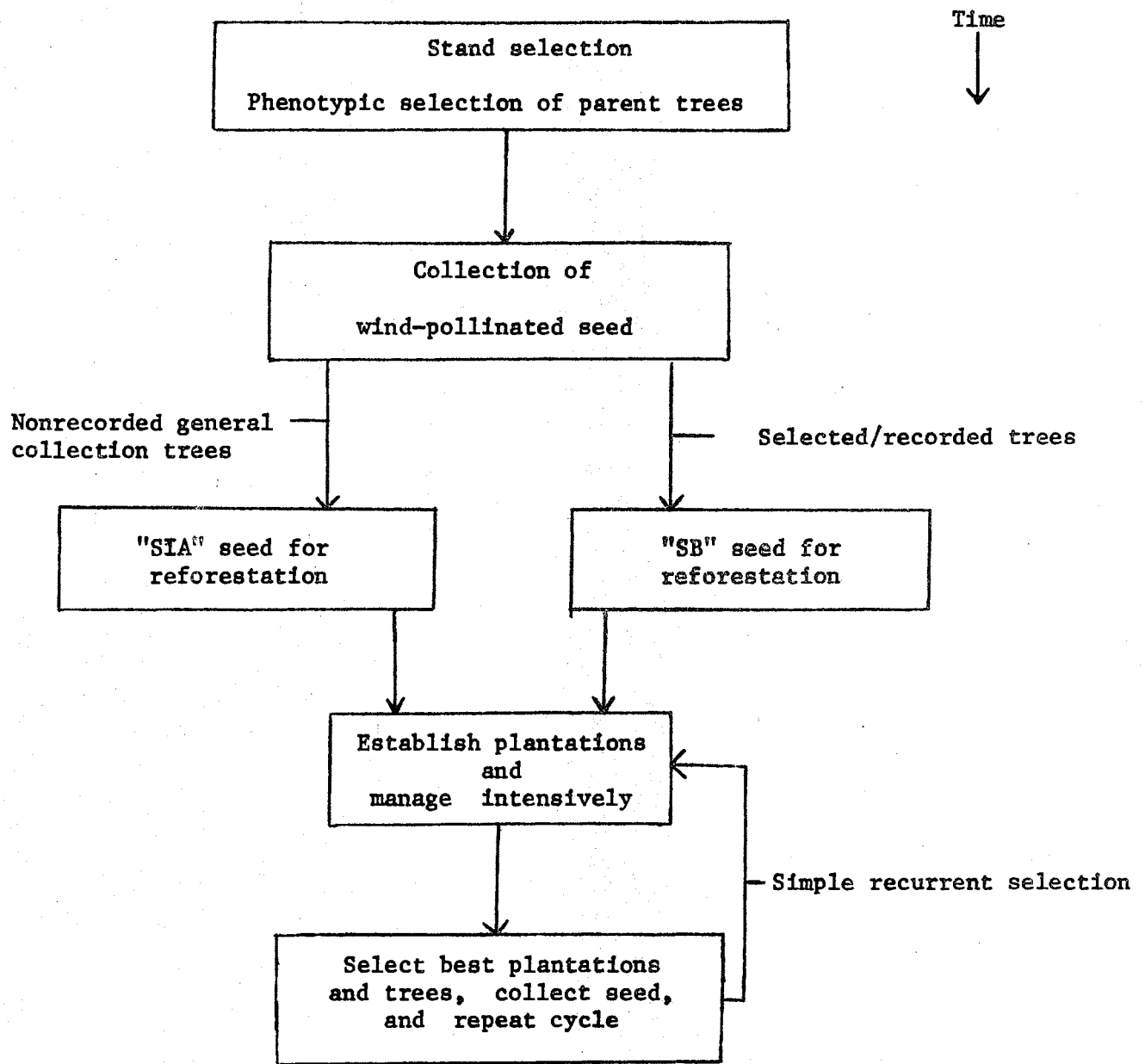


Figure 1. -- Extensive (low level) program flow chart.

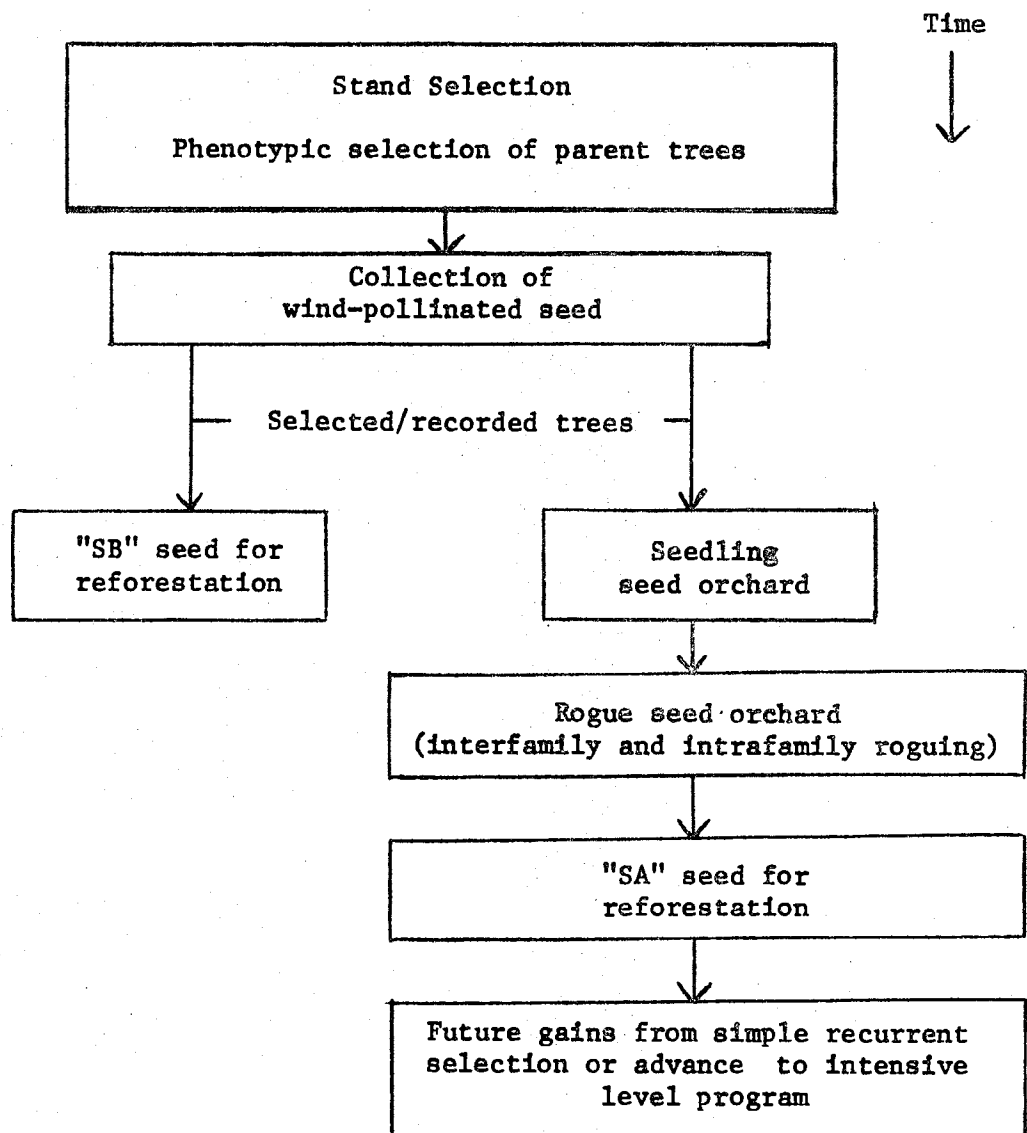


Figure 2. - Intermediate (mid-level) program flow chart.



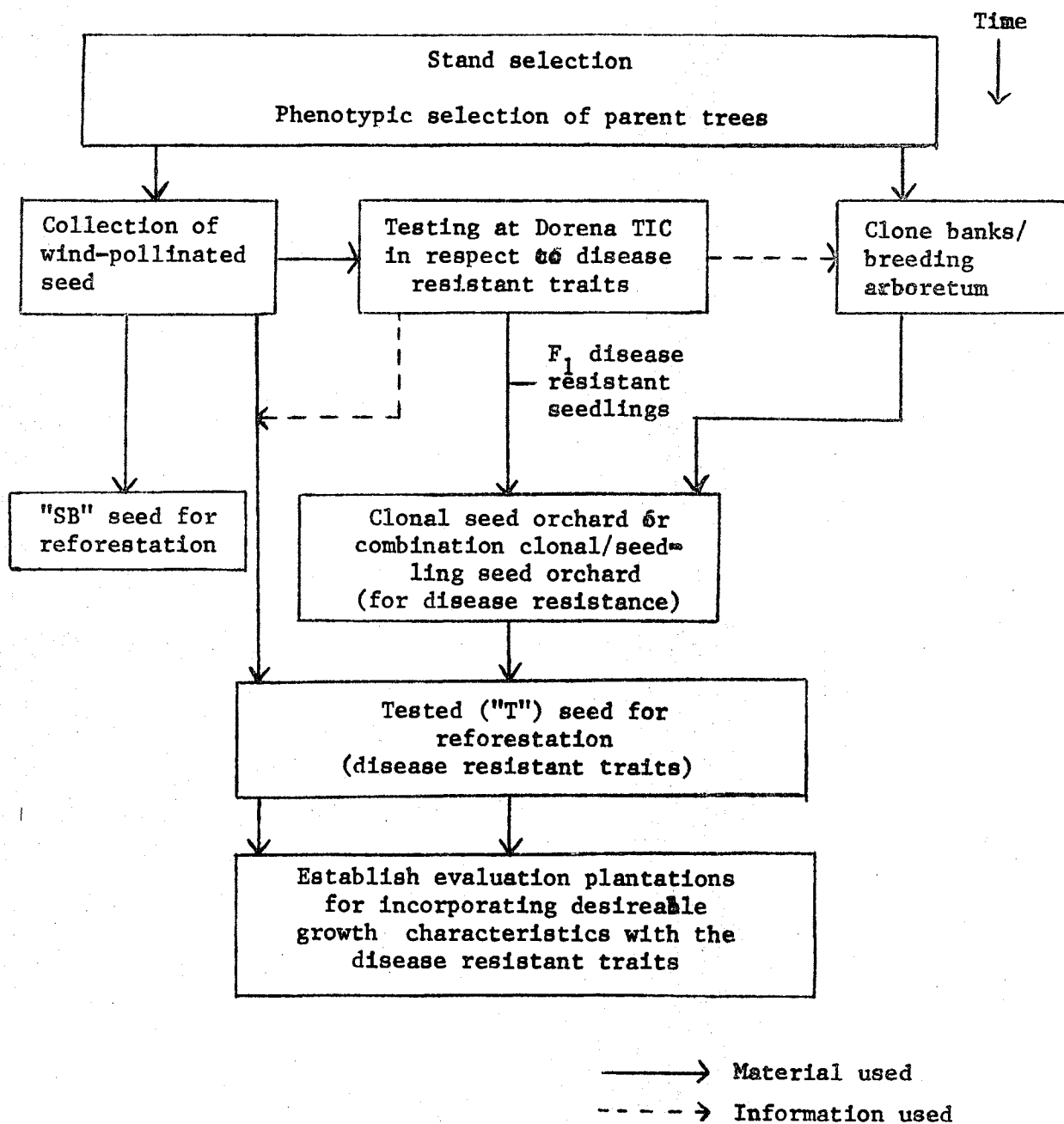


Figure 3. - Intensive (Disease resistant level) program flow chart.

plans within Regional guidelines and standards. (FSM 2475.11) However, since the program encompasses a great number of activities, Forest and Ranger District personnel are responsible for on-the-ground implementation of the program plan. The Program Geneticist will provide genetic/technical direction and serve as liaison for the Regional Geneticist.

Table 5. outlines the responsible personnel for major activities associated with the white pine resistant program on a regional level.

Table 6. outlines the organizational chart of the Dorena Tree Improvement Center. The mission of the Center has four main elements:

1. Develop resistant strains of white pines.
2. Develop resistant strains of lodgepole pine for Western gall rust resistant pine.
3. Extract all tree improvement seed for all species within the Region.
4. Provide technical guidance and direction to Tree Improvement Personnel on Forests and Districts.

#### Sugar Pine, Western White Pine Cooperative Tree Improvement Programs

It is Forest Service policy to encourage state, other Federal agencies, and private land holders in their tree improvement programs by taking part in cooperative agreements to exchange reproductive material. A memorandum of understanding exist between R-6 and the Bureau of Land Management (BLM), Medford Corporation and the Oregon State Department of Forestry. The agreement with BLM covers exchange of ~~repp~~reproductive material as well as testing of select parent trees on BLM land. (Appendix A exhibit 1). The agreements with the Oregon State and Medford Corporation cover exchange of reproductive material only (Appendix A, exhibit 2,3).

An agreement between Burlington Northern and Forest Service is in preparation. National Forests that share breeding zones coordinate their

Table 5. Major Activities of the White Pine Breeding Program

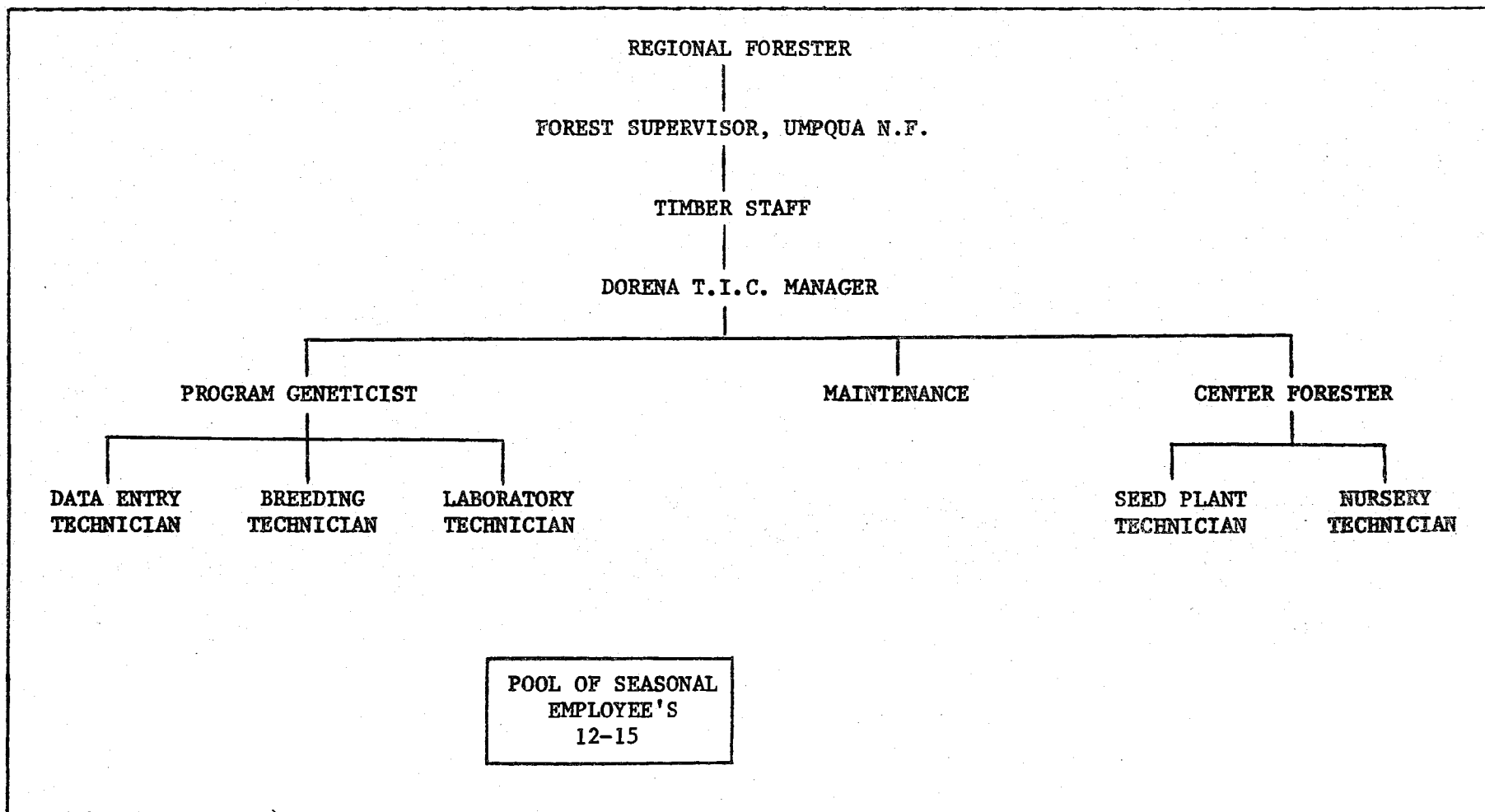
Responsible Personnel	Tree Improvement Plan	Forest Genetics Direction	Phenotypic Selection & Maintenance	Collection of O.P. Seed	Nursery Program Testing	Selection in Program Test	Seed <u>2/</u> Orchard & Arboretum	Evaluation Plantations <u>3/</u>
							a b c d	a b c
Regional <u>1/</u> Geneticist	X	X			X	X	X X	X
D.T.I.C. <u>1/</u> Geneticist	X	X			X	X	X X X	X
Tree Improvement Specialist at S.O.	X		X	X			X X	X X
Tree Improvement Specialist at Ranger District	X		X	X			X X	X X

1/ Technical direction and guidance for all aspects of applied Forest Genetics principles specially those pertaining to breeding or disease resistance.

2/ a. selection of location; b. preparation, establishment, maintenance, measurements/records; c. selection of Genotypes; d. design and advanced generation breeding schemes.

3/ a. selection of location; b. preparation, establishment, maintenance, measurements & records; c. design and analysis of data.

Table 6. Organizational Chart for the Dorena Tree Improvement Center



tree improvement activities to eliminate duplication of effort. Each Forest has a responsibility to perform its share of work load.

Tables 7 and 8 illustrate how work load are being shared between Forests through coordination of efforts.

#### AN OPERATIONAL PLAN FOR REGION 6 RUST RESISTANCE PROGRAM

##### Stand Selection

Selection will be done only on national forest land except where approval has been granted through written agreement among cooperators. Selection of a good stand can make the program more efficient; a "Good" stand is one that approximates a managed stand. Since good stand growth and adaption are both important traits, the age of the stand should be from one-fourth to full rotation age. The majority of stands should be 25+ years of age. This criteria ensures that all trees have been exposed to natural inoculation by the rust fungus for at least 25 years.

##### Selection Intensity

Prior to 1970, selection criteria was "simple"; select clean uninfected candidates. Most of the trees selected were in groups of 10 to 20 candidates within a few yards of each other. In 1970, the Region took another look at the selection methods and criteria. There was more knowledge available about the white pine-rust complex, and the Regions' philosophy stressed greater genetic breadth. Accordingly, selection methods and criteria changed to envelop both genetic breadth and resistance stability. Depending on intensity level of program, the number of selected parents per breeding zone ranges from 50 trees to 600 on national forest land.

The selected phenotypically desirable trees have served and will serve as the initial seed source for genetically superior stock. Genetic gains

Table 7. Number of Selected Tree Goal for Western White Pine and Sugar Pine in Breeding Blocks 4 and 5.

Breeding Zone	Select Tree Goal		Total # Acres on F.S. (X 1000)	% of Acres on Rogue River	Select Tree Goal on Rogue River	% of Acres on Umpqua	Select Tree Goal on Umpqua	% of Acres on Siskiyou	Select Tree Goal on Siskiyou
	BLM	F.S.							
119-00043	22	178	14.6	63	112	37	-	-	-
119-00044	2	198	164.8	54	107	46	91	-	-
119-00045	6	194	192.3	54	105	46	89	-	-
119-00046	-	100	94.3	53	53	47	47	-	-
119-00053	-	50	3.8	0	0	-	-	100	50
119-00054	-	50	4.3	0	0	-	-	100	50
119-00055	-	50	21.3	97	49	-	-	3	1
117-00043	34	176		15	26	85	150	-	-
117-00044	42	158		51	81	49	77	-	-
117-00045	2	198		74	147	26	51	-	-
117-0052	144	56	23.4	3	2	-	-	97	54
117-0053	176	24	58.6	34	8	-	-	66	16
117-00054	48	152	62.7	57	87	-	-	43	65
117-00055	-	200	27.6	86	172	-	-	14	28

Table 8. Sugar Pine and Western White Pine Seed Orchards Planned for Breeding Blocks 4 and 5.

Breeding Zone	Name of Seed Orchard	Seed Orchard Location	Yr/Establishment
117-10043 -15043		Umpqua N.F.	
117-10044 -15044	Junction	Rogue River N.F.	1987
117-10045 -15045	Zimmerman	Rogue River N.F.	1984
117-10052 -11052		Siskiyou N.F.	
117-10053 -11053		Siskiyou N.F.	
117-11054 -10054	Horse Mtn.	Siskiyou N.F.	1982
117-10055 -11055	Upper Middle Fork Applegate	Rogue River N.F.	1987
119-10043 -15043		None	
119-10044 -15044	Jim Creek	Rogue River N.F.	1980
119-10045	Dailey Prairie	Rogue River N.F.	1982
119-10046		None	
119-10055		None	
119-10055		None	

will be achieved by selecting outstanding individuals, testing their ability to transmit these desirable traits and establishing seed orchards for interbreeding among the best parents.

#### Distribution of Selections

The selections should be distributed throughout the respective breeding zones. Selections should be at least one-fourth mile apart.

#### Individual Tree Selections

Selected trees should exhibit desirable characteristics. The number of cankers that are allowable on candidate trees depends on the intensity of rust in the stand. The criteria for selecting trees is as follows:

- a. Western white pine (Hoff and McDonald, 1980, Tree Improvement Training Paper, No.5)

<u>Rust intensity in the stand (Average number of cankers/tree)</u>	<u>Maximum allowable infection per candidate (number of live or dead cankers)</u>
10 - 20	None
21 - 40	1
41 - 75	2
76 - 150	3
151+	4-5

- b. Sugar pine

The number of cankers on sugar pine trees in the forest is usually much lower than on western white pine under similar blister rust hazard conditions. Therefore, the following guidelines are recommended.

<u>Rust intensity in the stand (average number of cankers/tree)</u>	<u>Maximum allowable infection per candidate (number of live or dead cankers)</u>
1 - 10	None
11 - 20	1
21 - 40	2
41 - 75	3
76+	4-5



Priority for selection of a candidate tree from a stand with acceptable number of cankers is:

1. Infected trees exhibiting both or either slow canker growth and/or tolerance.
2. Trees free from blister rust cankers.

Form - The select tree should exhibit straight bole, good form class for the site/stand condition. Runty, seriously deformed (especially multi-forked) trees should be avoided. Do not select seriously diseased (other than blister rust) or seriously insect damaged trees. Trees with sinuous and crooked stems not associated with likely mechanical injuries should be avoided because these poor traits should be inherited.

Growth - All selected trees must have desirable growth characteristics. The candidate tree with the best height growth, diameter and form class will be chosen.

Cone Production - Any tree selected must show evidence of cone production. It is not imperative for the tree to have a cone crop when selected, but the tree should be able to provide a pickable cone crop for use in the testing program. Depending on test results, the potential select tree may be the one used in seed orchards.

#### Records

Keeping accurate up-to-date records is extremely important in a tree improvement program. Every select tree should have a "Selected Tree Register (STR)" form #R6-2470-109 (5/74) (Exhibit 1). All parts of the form should be filled out.

The trees in the field should be appropriately tagged and marked in the field. Accurate mapping of locations should be done on the back of the register form in order to relocate the select tree in the future.

An original copy of the STR should be kept at the District Office. Two photocopies sent to Supervisor's Office to be distributed as follows:

1. Supervisor's Office copy.
2. Dorena Tree Improvement Center copy delivered with seed lot.

All select trees should be made part of the new ADP system "Select Tree Data Base" developed for Region 6.

#### Technical Consideration

The breeding program for rust resistance in Region 6 rests on the accomplishments already made in over 26 years of selection, breeding, testing and attempts to bring the problems identified into a clearer focus to set future direction. It also builds on research findings and recommendations of scientists at the Intermountain Experiment Station (INT) and the Pacific Southwest Station (PSW).

The progeny tests of selected candidates at Dorena Tree Improvement Center and research done at INT have clearly indicated the presence of a number of resistance mechanisms in the white pine-blister rust system, (Hoff and McDonald, 1980). The resistance mechanisms in this disease complex could be divided into two categories: vertical resistance or sometimes referred to as specific resistance and horizontal resistance or generalized resistance. Vertical resistance is a race specific function against certain rust races or biotypes but not against others. Generalized resistance (race nonspecific) functions against all biotypes. The multifactor lines, set as goals for populations of white pine in Region 6 are designed to develop a stable population which is characterized by a number of non-specific resistance mechanisms. Maintenance of a broad genetic base in the population is the basis of all activities of the tree breeding program. It may be better to refer to these lines as multimodal lines rather than multi-

factor lines which could be confused with multiline varieties. The multimodal resistance varieties have the ability to contain the rust population at a low level rather than provide an environment favorable for evolution and selection of virulent races of rust that are capable of undermining resistant varieties with only specialized resistance. The area around the Champion Mine on the Umpqua National Forest has provided us with an excellent example of the devastating effect a new strain of rust can have on a population of western white pine. Historically, the white pine population in the Champion Mine area provided the program with a number of resistant candidates. During the early seventies, many of the previously resistant selections developed cankers and died so now the whole population is nearly eliminated. A study with INT revealed that the new strain of rust which developed in that area negates the unimodal resistance mechanism, namely the needle shed mechanism, which provided the main source of protection to that population. A change in genetic makeup and frequency in the rust population, especially one of the virulent strains, has affected mechanisms of resistance and caused dwarfism within the progeny of some of the families exposed to that inoculum.

Our experience with the rust system has provided the region with several options for the production program:

1. The region has the genetic potential to utilize different levels of resistance in its planting stock. These levels of resistance are identified in the region as low, intermediate and high-level resistance. When these resistance levels are matched with appropriate rust hazard conditions, risks in reforestation with the white pines are greatly reduced. The program this far has identified a number of good transmitters of rust resistance in both sugar pine and western white pine. Survival rates of up to 60% in open

pollinated families have been demonstrated (Table 9). Such material has been propagated for nine seed orchards in the region. These seed orchards serve 15 breeding zones. (Table 10).

2. Region 6 thus far has been using open pollinated seed from tested parents, that demonstrated some resistance, for reforestation. Since 1964 western white pine has been used in 66 plantations around the region. Data from rust infection surveys in these plantations will be used in delineating hazard zones.

#### Blister Rust Hazard Zones

Despite the presence of blister rust in the Region for over 80 years, we still lack a clear definition of the magnitude of the problem. Within the Region, there is a great variation in the incidence and impact of blister rust. There is also considerable variation of hazard within the breeding zones depending on land physiography, position (aspect) and proximity from streams of the site on the slope, and other environmental and ecological factors that could be favorable to serious infection (Quick, 1962).

Undoubtedly, there are many sites in the Region where the risk is low enough that genetic resistance need not be considered. For these reasons, the pest management group at the Regional Office in cooperation with the Dorena Tree Improvement Center, has started to delineate rust hazard zones. The objective is to assign risk factors, so that resistance breeding material can be allocated to areas which show the greatest promise. We are now looking at broad hazard classifications such as low, medium and high.

#### Screening Phase of the Rust Resistance Breeding Program

Progeny of all western white pine and sugar pine select trees go through the first stage of progeny testing, that is the screening program of all par-

Table 9. Survival (%) of Some Open Pollinated Sugar Pine Families from the Nursery Tests after Seven Growing Seasons.

Family #	% Survival
1	34
2	30
3	5
4	55
5	8
6	46
7	11
8	61
9	52
10	4

Table 10. Western White and Sugar Pine Seed Orchards in Region 6.

Species 1/	Seed Orchard	National Forest	Breeding Zone(s)	# of Clones
119	Coyote	Gifford Pinchot	00014 00015 00022 00023 00024	129
119	Pebble Creek	Willamette	00033 00034 00035	84
119	Crane	Fremont	00187	71
119	Jim Creek	Rogue River	00044	74
119	Dailey Prairie	Rogue River	00045	82
117	Zimmerman	Rogue River	00045	60
117	Junction	Rogue River	00044	150
117	Upper Middle Fork	Rogue River	00055	170
117	Horse Mtn	Siskiyou	00054	134

1/ 119 Western White Pine  
117 Sugar Pine

ents by artificial inoculation. The remainder of this section will include a description of the rust screening program protocols for Region 6.

### Inoculation System

Research (Bingham, 1972; McDonald and Hoff, 1980) provided us with a description of inoculation procedures useful for the environment at Moscow, Idaho. Region 6 started testing by using the Region 1 system but found it necessary to make some changes to adapt the inoculation procedures for Region 6 conditions. Rust disease represent perhaps the oldest know associations between host and pathogen. The biology and environmental conditions needed by the rust fungus to complete its life cycle are well documented in the literature (Day, 1972; Bingham, 1972; McDonald and Hoff, 1980).

The inoculation system of the region is based on the knowledge of rust biology and environmental needs for the development of the disease. It has been continuously upgraded and modified through the experience of the people working with the system and employing research results. The following is a brief description of the inoculation at the Center:

1. The seedlings are inoculated after the second growing season. At this age, the seedling of western white pine has mostly secondary needles with a few remnant primary leaves. Sugar pine exhibits the development of a late summer growth (lammas shoots) of up to 5 inches in some families which results in the presence of relatively high proportion of primary leaves. Much of the early resistance is in the secondary needles, the nature of primary needles and lack of much resistance in them enhances the rate of stem infections in sugar pine. Cultural regimes such as irrigation and soil media are being evaluated with respect to development of lammas shoots.

2. Inoculation at the center takes place when the development of rust fungus allows usage of the inoculum. In the Oregon environment the seedlings

are inoculated during the month of September and could last to the end of the first week in October.

3. For inoculation, the seedlings are placed in a chamber equipped with environmental controls for temperature and humidity. The relative humidity is kept at 100 percent and the temperature between 65-70°F. This is achieved by a system of two misters (a third is being installed) each equipped with 4 nozzles that operate under a pressure of 120 psi and two air conditioners.

4. Both inoculum from a Ribes garden at Dorana TIC and natural sources from several areas are used for the inoculation. All sources are mixed thoroughly while leaves are spread around, with telia-bearing side down, on wire screens 2 feet above the seedlings.

5. Leaves are covered with a plastic tent. The tent eliminates runoff water accumulation on the leaves and the monitoring slides.

6. Microscopic slides covered with a thin layer of rubber cement are placed among the seedlings to facilitate monitoring of inoculum density.

7. Test conditions are maintained until an inoculum density of 3000 spores and 4500 spores per centimeter square for the western white pine and sugar pine respectively are applied. The seedlings are left in the same environmental condition 12 more hours after inoculation to insure germination of the basidio spores.

Thus far the facilities has been capable of handling the progeny test of all available seed lots of western white pine and sugar pine in Region 6.

#### Rust Inspection

The methods of rust inspection, outlined in Table 11, permits the ranking of families according to the different types of horizontal resistance. It also permits the selection of individuals with vertical resistance mech-



**Table 11. Inspection Schedule for Collection of Resistance Data after Inoculation of Western White Pine and Sugar Pine Seedlings.**

Inspection	Date of Inspection	Data Collection and Resistance Mechanisms
First Inspection	June following previous fall inoculation	<p>Reduced needle lesion frequency in secondary needles</p> <p>No spot formation in secondary needles</p> <p>Early shed of infected secondary needles</p>
Second Inspection	September 1 year after inoculation	<p>Early shed of infected secondary needles</p> <p>Fungicidal reaction in the short shoot</p>
<p>Third Inspection</p> <p>Fourth Inspection</p>	<p>September 3 years after inoculation</p> <p>September 4 years after inoculation</p>	<p>Canker formation, slow fungus growth in secondary needles <u>1/</u></p> <p>Necrotic area of sunken bark definitely associated with the base of a needle bundle, bark reaction</p> <p>Any stem reactions, bark reaction</p> <p>Slow fungus growth and tolerance in stem</p> <p>Sporulation</p> <p>Dead or alive</p> <p>Stunted or normal growth</p> <p>Selection for seed orchard</p>

1/ Slow fungus growth in secondary needles is not actually tallied, it is derived from canker formation data based on time interval between needle infection and canker formation.

anisms from these families. Analysis of first year data, frequency of needle infection, permits ranking of families from lowest to highest number of infections. Families with lowest number of lesions are recommended to be used as a seed source for reforestation.

A ranking of families is made according to the presence of other resistance mechanisms. Selection of the families for seed orchard use is based on the following guidelines:

1. Select families with highest combination of horizontal resistance mechanisms.
2. Resistant population should not be based on a single gene, diversity is essential.
3. Whenever possible, include material with vertical resistance types to maintain a low gene frequency of these types. A high gene frequency of this resistance mode results in selection pressure on the rust population which may mutate, resulting in a new strain of rust being formed that eliminates the whole population.

With the above guidelines in mind, the data is used to select seed orchard trees as follows:

1. Family selections for reduced frequency of needle infections.
2. Family selections for slow fungus growth in the secondard needles.
3. Family and within Family selections for slow fungus growth or tolerance in the stem.
4. Individual selections for premature shedding of infected needles, short shoot reactions and bark reactions.

In summary, family selection is mainly used for the horizontal mechanisms while individual selection is used for material with vertical resistance.

At the present time, the testing program has produced 639 and 620 western white and sugar pine families respectively, propagated in 9 seed orchards in the region (Table 10 page 23).

Doc. No. 2408A

3 Draft

INTER-AGENCY AGREEMENT

BETWEEN

OREGON STATE OFFICE,

BUREAU OF LAND MANAGEMENT, U.S.D.I.

AND

REGION 6, FOREST SERVICE, U.S.D.A.

FOR

SOUTHERN OREGON

SUGAR PINE AND WESTERN WHITE PINE

TREE IMPROVEMENT COOPERATIVE

This agreement is entered into by and between the Department of Interior, Bureau of Land Management, hereinafter referred to as BUREAU, acting by and through the State Director of Oregon under the authority of the Public Lands Administration Act P.L. 86-649, Stat. 506-43 U.S.C. 1361; and the Department of Agriculture, Forest Service, hereinafter referred to as the SERVICE, acting by and through the Regional Forester, Pacific Northwest Region, under authority of the Multiple-Use Sustained Yield Act, 16 U.S.C. 528-531, the White Pine Blister Rust Protection Act of April 26, 1940, 54 Stat. 168, 16 U.S.C. 594a, AND Section 601, Economy Act of June 30, 1932, 31 U.S.C. 686, 686b.

WHEREAS, it is SERVICE policy and BUREAU policy for its National Resource Lands to:

1. Encourage states, other Federal agencies, and private landholders in their tree improvement programs by making vegetative and sexual propagating materials available to them from selected trees on their land to the extent they are not needed by the SERVICE or the BUREAU for its use provided there is no resultant conflict with other SERVICE or BUREAU uses or other regulations.

2. Cooperate with states, Federal agencies, and private landholders in establishing standards and specifications for superior trees and in maintaining records of their locations, and other pertinent information concerning their use and performance in production of genetically improved seed.

WHEREAS, under the White Pine Blister Rust Protection Act, the SERVICE is charged with technical direction and leadership for all agencies in the conduct of white pine blister rust control programs.

WHEREAS, the SERVICE has facilities to evaluate white pine blister rust resistance factors in sugar pine and western white pine trees, and it is necessary to evaluate the trees under uniform conditions and <sup>so that</sup> for the ~~same~~ <sup>can be properly assessed</sup> resistance factors to provide optimum use for the development of white pine blister rust resistant strains of sugar pine and western white pine.

WHEREAS, the BUREAU is interested in producing white pine blister rust resistant strains of sugar pine and western white pine for their lands in the Medford and Roseburg Districts and the SERVICE is interested in doing the same on their lands for the Rogue River, Siskiyou, and Umpqua National Forests as follows:

Table 1 - Breeding Zones

Breeding Zone	Species	Elevation	Included Tree Seed Zones of the Western Tree Seed Council
117-00043	Sugar Pine	2,000-3,000	{ 481, 491, 492, 493, 501, 502, 701, 721
117-00044	Sugar Pine	3,000-4,000	
117-00045	Sugar Pine	4,000-5,000	
119-00043	Western White Pine	2,000-3,000	
119-00044	Western White Pine	3,000-4,000	
119-00045	Western White Pine	4,000-5,000	{ 072, 081, 082, 091, 270, 321, 511, 512
117-00052	Sugar Pine	1,000-2,000	
117-00053	Sugar Pine	2,000-3,000	
117-00054	Sugar Pine	3,000-4,000	
119-00054	Western White Pine	3,000-4,000	

Table 2 - Acreage Suitable for White Pine

		Acreage Distribution		
Project	Acres	Percent of Total	SERVICE	
			M. Acres	Percent of Total
117-00043	28.8	17	137.4	83
117-00044	22.2	21	84.1	79
117-00045	0.6	1	39.5	99
119-00043	6.1	11	51.0	89
119-00044	1.0	1	100.7	99
119-00045	2.8	3	98.7	97
117-00052	36.0	72	14.0	28
117-00053	95.8	88	12.5	12
117-00054	19.5	24	61.5	76
119-00054	0.5	3	17.0	97



A. NOW, THEREFORE, in consideration of the above premises, the parties hereto respectively agree that they will:

1. Select white pine blister rust resistant candidate sugar pine and western white pine trees on their land holdings in accordance with mutually agreed upon standards <sup>which is based on past scientific findings</sup> until the following minimum number of tested white pine blister rust resistant trees are available:

Breeding Zone	Minimum Number of Tested White Pine Blister Rust Resistant Trees in Parental Generation				
	BUREAU		SERVICE		Umpqua
	Medford	Roseburg	Rogue River	Siskiyou	
117-00043	17	17	83	-	83
117-00044	2	21	79	-	79
117-00045	1	1	99	-	99
119-00043	11	11	89	-	89
119-00044	1	1	99	-	99
119-00045	3	3	97	-	97
117-00052	144	-	28	28	-
117-00053	176	-	12	12	-
117-00054	48	-	76	76	-
119-00054	6	-	97	97	-

2. Make location records of the selected trees in the parental and subsequent generations available to all other parties hereto in this agreement.

3. Harvest, process, and store seed from the selected trees on their lands and make a portion of said seed available to the SERVICE's Dorena Tree Improvement Center for sowing by the SERVICE for evaluation for resistance to white pine blister rust.

4. Make forest tree reproductive materials from trees selected as part of this Memorandum of Understanding available to all other parties hereto for tree improvement purposes to the extent that they are not needed by the donating party and provided that there is no resultant conflict with other uses and policy of the donating party.

5. Perform such crosses between selected trees on their lands as are necessary to advance the development of white pine blister rust resistant sugar pine and western white pine in accordance with a mutually agreed upon crossing plan. This includes, but is not limited to, trees in the forest (original selection), in breeding arboreta, in seed orchards, and in evaluation plantations.

6. Pursue the goal of developing multifactor lines containing both horizontal and vertical resistance factors ~~for seed orchard use as~~

Follows:

Line 1	Line 2	Line 3
Reduced Needle Lesion Frequency	Reduced Needle Lesion Frequency	Reduced Needle Lesion Frequency
Slow Canker Growth	Slow Canker Growth	Slow Canker Growth
Tolerance	Tolerance	Tolerance
Early Shed of Infected Needles	Short Shoot Reaction	Bark Reactions

7. Develop seed orchards as needed to produce tree seed for reforestation use on their lands and make any excess tree seed produced available for purchase by the other party to this agreement.

8. Protect and care for trees in breeding arboretums on their lands.

9. Develop evaluation plantations on their lands as mutually agreed upon to evaluate tested blister rust resistant trees for growth characteristics and field levels of resistance to white pine blister rust. The evaluation plantations will be distributed between the parties to this agreement based on the percentage of forest land in Table 2.

10. Assume financial responsibility for all work on their own lands except as provided in Sections B1 and B2 of this agreement.

11. Assume risks of loss of their seed sent to and of seedlings grown therefrom at the Dorena Tree Improvement Center.

B. It is mutually agreed and understood by and between the said parties that:

1. The SERVICE will:

a. Evaluate selected trees for resistance to white pine blister rust at the Dorena Tree Improvement Center in accordance with mutually acceptable standards and procedures.

b. Adjust sowing schedules for evaluation of selected BUREAU trees for resistance to white pine blister rust so as not to exceed the amount budgeted for this work by the BUREAU.

c. Make an annual report by July 1 to the BUREAU concerning the projected costs for the following fiscal year of carrying BUREAU trees already entered into the resistance evaluation program at Dorena Tree Improvement Center and an update on the projected costs for the full evaluation of a selected tree by year in evaluation program that the costs are expected to occur.

d. Make an annual report to the BUREAU by July 15-  
concerning the status of and resistance factors found in BUREAU and  
SERVICE trees being evaluated for resistance to white pine blister rust  
under this agreement.

2. The BUREAU will:

a. Reimburse the SERVICE on a yearly basis for the cost  
of evaluating trees selected on BUREAU lands for resistance to white  
pine blister rust.

b. Advise the SERVICE of the amount expected to be  
budgeted for the evaluation of BUREAU trees for resistance to white  
pine blister rust by January 1 preceeding the fiscal year in which the  
funds are to be expended.

3. Nothing herein shall be construed as obligating the SERVICE  
or BUREAU to expend or as involving the United States in any contract  
or other obligations for payment of money in excess of appropriations  
authorized by law and administratively allocated for this work.

4. No contribution to the cooperative effort herein provided for shall entitle the BUREAU to any share or interest in the said tree improvement plant material located on SERVICE land other than the right to use the same under the regulations of the SERVICE, and in fulfilling the terms of this agreement. No contribution to the cooperative effort herein provided for shall entitle the SERVICE to any share or interest in the said tree improvement plant material located on BUREAU land other than the right to use the same under the regulations of the BUREAU and in fulfilling the terms of this agreement.

5. No Member of, or Delegate to Congress, or Resident Commissioner shall be admitted to any share or part of this agreement, or to any benefit that may arise therefrom; but this provision shall not be construed to extend to this agreement if made with a corporation for its general benefit.

6. No party to this Memorandum of Understanding shall be liable to the other for any loss, damage, personal injury, or death occurring in consequence of the performance of this agreement, except for negligent acts of either party, their agents, or their employees.

7. This agreement shall be effective upon execution by the parties hereto.

8. Any party to this agreement may terminate their portion of the agreement by providing 90 days written notice. Unless terminated by written notice, this agreement will remain in force indefinitely and may be amended at any time by mutual consent of the parties hereto.

9. This agreement terminates all previous agreements between the BUREAU and the SERVICE for the development of sugar pine and western white pine for resistance to white pine blister rust in the State of Oregon.

10. In WITNESS WHEREOF, the parties hereto have executed this agreement as of the last written date below.

\_\_\_\_\_  
Date

\_\_\_\_\_  
State Director of Oregon  
BUREAU OF LAND MANAGEMENT

\_\_\_\_\_  
Date

\_\_\_\_\_  
Regional Forester  
U. S. FOREST SERVICE, PACIFIC  
NORTHWEST REGION

MEMORANDUM OF UNDERSTANDING  
BETWEEN  
OREGON STATE DEPARTMENT OF FORESTRY  
AND  
USDA, FOREST SERVICE, REGION 6  
FOR  
EXCHANGE  
OF  
SUGAR PINE AND WESTERN WHITE PINE  
TREE IMPROVEMENT MATERIAL  
IN  
THE  
STATE OF OREGON



## MEMORANDUM OF UNDERSTANDING

This agreement is entered into by and between the Oregon State Department of Forestry, hereinafter referred to as STATE, acting by and through the State Forester; and the Department of Agriculture, Forest Service, hereinafter referred to as the SERVICE, acting by and through the Regional Forester, Pacific Northwest Region, under authority of the Multiple-Use Sustained Yield Act, 16 U.S.C. 528-531.

WHEREAS, it is SERVICE policy to:

1. Encourage states, other Federal agencies, and private landholders in their tree improvement programs by making vegetative and sexual propagating materials available to them from selected trees on National Forest land to the extent they are not needed by the SERVICE and provided there is no resultant conflict with other SERVICE uses or other regulations.
2. Cooperate with states, Federal agencies, and private landholders in tree improvement programs which will be mutually beneficial and in establishing standards and specifications for superior trees and in maintaining records of their locations, establishment of evaluation plantations, and sharing of knowledge concerning use and performance of improved forest reproductive materials.
3. Cooperate with and seek the cooperation of nonfederal agencies, concerns, and individuals when it is in the public interest, is administratively desirable, and is currently authorized by law, directly or by implications; and

WHEREAS, the STATE, and the SERVICE have forest landholdings in the State of Oregon; and

WHEREAS, the STATE, and the SERVICE wish to cooperate in sugar pine and western white pine genetic tree improvement involving STATE lands and National Forest lands in Oregon; and

WHEREAS, such cooperation will be mutually beneficial to the STATE and the SERVICE:

A. NOW, THEREFORE, in consideration of the above premises, the parties hereto agree that they will respectively:

1. Make sugar pine and western white pine forest tree improvement materials from trees selected for genetic tree improvement purposes in the cooperative area available to the other party hereto in the cooperative area for tree improvement purposes to the extent that they are not needed by the donating party and provided that there is no resultant conflict with other uses and policy of the donating party.

2. Provide a mutually acceptable working plan to the other party and obtain any required permits from the other party prior to the selection of trees located on the other parties land for genetic tree improvement purposes and prior to the collection of forest reproductive material for tree improvement purposes from selected trees located on the land of the other party.

3. Share knowledge concerning use and performance in tree improvement programs of forest reproductive material obtained from selected trees as part of this agreement.

4. Make location records of the selected trees from which forest reproductive material is obtained as part of this agreement available to the other party in this tree improvement cooperative upon request by that party.

5. Assume financial responsibility for all work performed in the cooperative area by themselves, their employees, and their agents.

B. It is mutually agreed and understood by and between the said parties that:

1. Nothing herein shall be construed as obligating the Forest Service to expend or as involving the United States in any contract or other obligations for payment of money in excess of appropriations authorized by law and administratively allocated for this work.

2. No contribution to the cooperative effort herein provided for shall entitle the STATE to any share or interest in the said tree improvement plant material located on SERVICE land other than the right to use the same under the regulations of the SERVICE, and in fulfilling the terms of this agreement. All tree improvement plant material located on SERVICE lands shall be and remain the property of the United States. Neither shall the SERVICE have any share of interest in said tree improvement plant material located on STATE lands, except as provided by the STATE, and in fulfilling the terms of this agreement. All tree improvement plant material located on STATE lands shall be and remain the property of the STATE.

3. Neither the STATE nor the SERVICE makes any claim concerning the genetic superiority of untested selected trees included in this agreement.

4. Nothing herein shall be construed as authorizing either the STATE or the SERVICE to culture selected trees on the other's land. The culture of selected trees includes release, fertilization, use of chemicals to induce seed productions, control of cone and seed insects, etc.

5. Each party will direct its own actions and resources, there will be no exchange of funds, goods, personnel, or services.

6. No Member of, or Delegate to Congress, or Resident Commissioner shall be admitted to any share or part of this agreement or to any benefit that may arise therefrom; but this provision shall not be construed to extend to this agreement if made with a corporation for its general benefit.

7. No party to this Memorandum of Understanding shall be liable to the other for any loss, damage, personal injury, or death occurring in consequence of the performance of this agreement, except for negligent acts of either party, their agents, or their employees.

8. This agreement shall be effective upon execution by the parties hereto.

9. Any party to this agreement may terminate their portion of the agreement by providing 90 days written notice. Unless terminated by written notice, this agreement will remain in force indefinitely and may be amended at any time by mutual consent of the parties hereto.

4.22-81

Date

H. B. Oak

State Forester

Oregon State Department of Forestry

5-11-81

Date

James F. Terrence

for Regional Forester

USDA Forest Service, Pacific

Northwest Region

MEMORANDUM OF UNDERSTANDING  
BETWEEN  
MEDFORD CORPORATION  
AND  
USDA, FOREST SERVICE, REGION 6  
FOR  
EXCHANGE  
OF  
SUGAR PINE  
TREE IMPROVEMENT MATERIAL  
IN  
JACKSON COUNTY  
STATE OF OREGON

## MEMORANDUM OF UNDERSTANDING

This agreement is entered into by and between the Medford Corporation, hereinafter referred to as MEDCO acting by and through the Vice President; and the Department of Agriculture, Forest Service, hereinafter referred to as the SERVICE, acting by and through the Regional Forester, Pacific Northwest Region, under authority of the Multiple-Use Sustained Yield Act 16 U.S.C. 528-531.

WHEREAS it is SERVICE policy to:

1. Encourage states, other Federal agencies, and private land-holders in their tree improvement programs by making vegetative and sexual propagating materials available to them from selected trees on National Forest land to the extent they are not needed by the SERVICE and provided there is no resultant conflict with other SERVICE uses or other regulations.
2. Cooperate with states, Federal agencies, and private land-holders in tree improvement programs which will be mutually beneficial and in establishing standards and specifications for superior trees and in maintaining records of their locations, establishment of evaluation plantations, and sharing of knowledge concerning use and performance of improved forest reproductive materials.
3. Cooperate with and seek the cooperation of nonfederal agencies, concerns, and individuals when it is in the public interest, is administratively desirable, and is currently authorized by law, directly or by implications; and

WHEREAS MEDCO, and the SERVICE have forest landholdings in Jackson County Oregon; and

WHEREAS, MEDCO, and the SERVICE wish to cooperate in sugar pine genetic tree improvement involving MEDCO lands and National Forest lands in Jackson County Oregon; and

WHEREAS such cooperation will be mutually beneficial to MEDCO and the SERVICE:

A. NOW, THEREFORE, in consideration of the above premises, the parties hereto agree that they will respectively:

1. Make sugar pine forest tree improvement materials from trees selected for genetic tree improvement purposes in the cooperative area available to the other party hereto in the cooperative area for tree improvement purposes to the extent that they are not needed by the donating party and provided that there is no resultant conflict with other uses and policy of the donating party.

2. Provide a mutually acceptable working plan to the other party and obtain any required permits from the other party prior to the selection of trees located on the other parties land for genetic tree improvement purposes and prior to the collection of forest reproductive material for tree improvement purposes from selected trees located on the land of the other party.

3. Share knowledge concerning use and performance in tree improvement programs of forest reproductive material obtained from selected trees located on the land of the other party.

4. Make location records of the selected trees in the cooperative area available to the other party in this tree improvement cooperative upon request by the other party.

5. Assume financial responsibility for all work performed in the cooperative area by themselves, their employees, and their agents.

B. It is mutually agreed and understood by and between the said parties that:

1. Nothing herein shall be construed as obligating the Forest Service to expend or as involving the United States in any contract or other obligations for payment of money in excess of appropriations authorized by law and administratively allocated for this work.

2. No contribution to the cooperative effort herein provided for shall entitle MEDCO to any share or interest in the said tree improvement plant material located on SERVICE land other than the right to use the same under the regulations of the SERVICE, and in fulfilling the terms of this agreement. All tree improvement plant material located on SERVICE lands shall be and remain the property of the United States. Neither shall the SERVICE have any share of interest in said tree improvement plant material located on MEDCO lands, except as provided by MEDCO, and in fulfilling the terms of this agreement. All tree improvement plant material located on MEDCO lands shall be and remain the property of MEDCO.

3. Neither MEDCO nor the SERVICE makes any claim concerning the genetic superiority of untested selected trees included in this agreement.

4. Nothing herein shall be construed as authorizing either MEDCO or the SERVICE to culture selected trees on the other's land. The culture of selected trees includes release, fertilization, use of chemicals to induce seed productions, control of cone and seed insects, etc.

5. Each party will direct its own actions and resources, there will be no exchange of funds, goods, personnel, or services.



6. No Member of, or Delegate to Congress, or Resident Commissioner shall be admitted to any share or part of this agreement or to any benefit that may arise therefrom; but this provision shall not be construed to extend to this agreement if made with a corporation for its general benefit.

7. No party to this Memorandum of Understanding shall be liable to the other for any loss, damage, personal injury, or death occurring in consequence of the performance of this agreement, except for negligent acts of either party, their agents, or their employees.

8. This agreement shall be effective upon execution by the parties hereto.

9. Any party to this agreement may terminate their portion of the agreement by providing 90 days written notice. Unless terminated by written notice, this agreement will remain in force indefinitely and may be amended at any time by mutual consent of the parties hereto.

2-12-81  
Date

3-25-81  
Date

R. E. Keene  
Vice President  
MEDFORD CORPORATION

D. L. Waltham  
Regional Forester  
U. S. Forest Service, Pacific  
Northwest Region

## Resistance Research at the Pacific Northwest Station

Roy R. Silen

Historically, the PNW Station has had no sustained program in resistance breeding. Considerable information has been produced however.

Going back to 1954 when the Genetics Project was initiated, there were only a few critical disease problems that might have merited research priority--white pine blister rust, root rot of Port Orford cedar, Sitka spruce weevil and balsam woolly aphid. At less critical levels practically every Northwest conifer has numerous pests that might need resistance breeding.

Since funding comes to our Station from Congress earmarked separately for Genetics and for Pest Research it was obvious at the start that joint efforts would be needed for any initial programs. In the early 1960's representatives from several disease and insect projects met with our Project in Portland to prepare a plan for a realistic level of research on each major pest on which resistance breeding might be done. The agreement at the outset was that work involving the insect or disease would be the responsibility of these projects, and activities involving breeding the plants would be our Project responsibility. This pattern has worked well in the sense of minimizing possible conflicts in deciding who does what. The pattern has worked poorly, however, in stimulating an active research effort.

At the meeting in the early 1960's we outlined efforts in several pest resistance areas:

White pine blister rust: Both the PSN Station and the group at Moscow, Idaho, were active in this field. Our view was that since research at the Moscow center was serving Region 6 breeding, they should continue leadership in this activity. We have encouraged the Moscow group to increase their services to Region 6, and assisted them where possible. There has been no resistance breeding program by the PNW Station for white pine.

Sitka spruce weevil resistance: Planting of Sitka spruce has been discouraged primarily by its proclivity to be damaged by weeviling. Here was a breeding project that was a natural for our Station. Insect research under Ken Wright had already identified three candidate trees on growth plots resistant to weeviling. We grafted scions from these trees at Cascade Head Experimental Forest, only to find that, as grafts, they were soon attacked by weevils. Meanwhile, a joint survey project of Region 6 and Meyerhaeuser Company searched thousands of acres for more resistant candidate trees, and found zero. With no resistant candidate trees the program has languished since about 1970.

Balsam Woolley Aphid: Although a plan was made, this program never got off the ground. Our Project surveyed the relative susceptibility of 23 *Abies* species at the Wind River Arboretum. Fraser and Corkbark fir were the most susceptible, with alpine fir the most susceptible of native Northwest trees. Noble fir seems virtually resistant. European species tolerated the woolley aphid without much effect.

The program planned was for silver fir, beginning with a search by insect projects, for candidate trees. This program was never funded.

Port Orford Cedar Root rot: Our Project from time to time, has cooperated with, and tried to support the lifetime research by Dr. Lew Roth search for resistance in Port Orford Cedar. The primary question over two decades has been whether resistance or even tolerance, existed in the Port Orford Cedar population. No certain evidence was ever produced.

We tried to organize a backcrossing program employing resistance of Asiatic species of *Chamaecyparis*. Our potential cooperators in Japan did not send us any pollen.

The more recent effort by Region 6 for a selection program seems more promising than earlier work, and our Station may tie into the effort should anything encouraging materialize.

Douglas-fir bark beetles: Although undoubtedly important, I have become personally convinced that bark beetles are more a symptom of drought than a breeding problem. Hence until someone convinces me otherwise, I do not see a role for resistance breeding.

Douglas-fir stem rots: For the record, we should note that the first genetic effort in the West had a pest resistance theme. When the Douglas-fir heredity study was planned in 1912 the primary question was whether seed from cull rotten trees was disgenic. The study, sown in 1912, and now approaching 70 years, has a large number of parents deliberately chosen to have had *Fomes pini*. Our records so far have shown 5 progeny to have *Fomes pini*, three from rotten parents and two from normal parents. Perhaps this large study with 5 outplantings from 120 parents will answer the question.

What I have covered up to now represents studies begun some time ago. Our five present active study areas have been somewhat more effective:

Browsing resistance to deer and hare: In cooperation with Ned Dimock of the Olympia Animal Damage Project, there was a series of studies that proved that a useful degree of resistance existed in each population we studied, which included the seed orchard at Dennie Ahl and a population near Corvallis. We demonstrated consistent, repeatable differences of over 2:1 in browsing between the progeny of various parents. Also the relative preference could be quantified, and actual browsing percentages would follow predictions of damage very closely. In fact, damage could be accurately modeled.

Last year, Bill Randall of the Siuslaw National Forest was able to test cuttings for resistance to deer browsing from the 250 parent trees represented in the Siuslaw Forests Beaver Creek Seed Orchard. Cooperation with our project for design and analysis and with the State Department of Fish and Wildlife for use of an orphan deer herd near Corvallis led to a successful identification of its most non-preferred top 10 percent of the clones. This will set up the Siuslaw Genetics project for incorporation of some level of deer browsing resistance in their planting stock.

This year we have gone considerably farther in gaining research information. Cuttings from progeny of a complex design of mating were tested with the same deer herd. We should be able to assess the additive, and non-additive genetic components of deer browsing resistance with this study design. This test should provide basic estimates of breeding efficiencies for future practical programs.

Christmas tree problems: Christmas tree growers are having greatly increased numbers of problems from pests as they enter second or even third generations on the same fields. Midge attacks causing damage to needles was reasonable well controlled with sprays. Mitchell of our laboratory, was able to show that there was considerable genetic differences in midge attack related to bud bursting date.

Rhabdocline disease became very prevalent in the plantings around Corvallis. Various spray schedules are used routinely now to handle the disease. Variations in susceptibility or resistance has been known for a long time, with high susceptibility of races from east of the Cascade Mountains, and generally best resistance observed in races from western Washington.

Other needle diseases are also serious like the "Benton County Crud" whose details of infection are not worked out. Nonetheless, spray schedules have been fairly effective control so far. Hence, the incentive to do breeding for resistance to these diseases has been quite low.

Swiss needle cast has reached serious proportions fairly recently. It, also, is being controlled with a spray called Bravo "500." Swiss needle cast has been known to have a similar geographic pattern of resistance to Rhabdocline disease. I will report later on some individual tree data on Swiss needle cast.

Phellinus weirii: Although our Station has long had a plan for investigating the genetic potentials of control for this root rot, we have been hung up for lack of a screening method. Recently Walt Theis began some studies to develop one, and with our Project, to assess possible resistance.

Fifty-half sib-families were planted over a bed of rotten wood originating from stumps of Phellinus infected trees. The hope was that when their roots were in contact with the rotten wood we would provide them drought stress and look for family mortality differences. None have developed so far. In fact, survival has been very high among the Douglas-fir seedlings. This has perplexed us.

Another series of tests with Douglas-fir families involves use of styroblocks, each with a 1" x 1" x 2" wooden block in the bottom. Half were cut from infected stumpwood, and half from non-infected. The first series with 10 families produced unusually promising results. Some families suffered almost complete kill or root damage was seen in contact with infected blocks. Other families had roots that grew around or even through the blocks with apparently no damage, even though subsequent isolations proved the rot was still active.

We repeated the test on a much larger scale--50 families. To make a long story short we got nothing. Not only were there no family differences in root damage of seedlings seen between infected and non-infected styroblock cells, we could not even isolate any fungus from the seriously infected blocks.

What this seems to show, considering the lack of results in the first and third experiment we do not have a screening method. However, the one good inoculation was dramatic in suggesting genetic differences in resistances. We would surely like to be able to get repeatable results.

Black stain: Of all the diseases of Douglas-fir that make me personally uneasy, black stain root rot, Verticillium dactylophila tops my list. I had only heard of it sketchily prior to 1979 when I first saw its symptoms on a genetics outplanting west of Corvallis. Walt Theis and I were asked to assess what was supposed to be Phellinus in a test plantation. Instead the 8 infected trees all had black stain. Since 1979 the infection has enlarged to 26 trees, and seems to be spreading actively ten feet per year. We are attempting to find all the infection centers in the more than 300 genetic test sites in our program to get early information on rate of spread.

What makes me uneasy is that black stain is a wilt--unlike other root rots of Douglas-fir. It isn't really established that it is a native disease even though it is now found over an extensive part of the Douglas-fir range. I certainly hope it is native. If it is introduced, kills trees as quickly as it does, and it spreads at the rate we observed, there is a cause to be concerned. Considering that there are continuous stands from California to British Columbia, this is one disease we need a handle on soon.

Swiss needle cast: I have save this one for last because the data we collected was so clear. I mentioned earlier that Christmas tree growers have witnessed an upsurge of Swiss needle cast. As described, the symptom is a "salt and pepper" appearance of 2nd-year needles as the block perthesia extrude from stomata in white lines along the underside of the needle.

Earl Nelson and I decided to sample needles from two plantations, one heavily infected, and the second we believed to be free of the disease. At least no problems had ever been reported. Nelson's crew counted the spots of fruiting bodies from 30 families in each plantation. Three trees were sampled from each replication per family. There were two replications at each of the two sites.

What we found was that every tree in every replication in both plantation had Swiss needle cast. In fact, an average of 26 fruiting bodies per millimeter of needle turned out to be the count. But what was very interesting is how the counts varied by parentage.

Here is our summary of the two factorial matings. Average needle spots per millimeter are shown for each cross, with the female parents A, B, C, D, E, and F shown on the right, and the male parents G, H, I, J, and K across the top. In the lower right corner in a box is the general average count--26 spots per millimeter. There isn't a lot of variation in the females--22 to 29 on the average. The males vary more--17 to 30.

What we see here is beautiful additive genetic variation--each parent contributing plus or minus to the average spotting according to its difference from the mean number of spots. Note first that parent J subtracts spots no matter what it was crossed with. In each case its cross with any of the 6 females gives less spots than the average parent. Parent G on the other hand raises spot numbers in 5 of the 6 crosses above the average of 26 spots. Parents J and K account for nearly all the crosses that are below the mean value of 26 and parents G, H, and I are above average in all but 3 cases of the total variation, 61 percent is explained by simple additive genetic variation.

Lest you think I am overimpressed by this, I believe this is a beautiful illustration of an artifact. What you are seeing is not an expression of resistance or susceptibility, but some morphological differences in the leaves so that some parentage expresses fewer, some more opportunities for a fruiting body to protrude out of a stomatal opening.

Every plant I have examined in the Corvallis area has Swiss needle cast. Most Douglas-fir show no ill effects. As Hadfield has noted, amounts of Perithecia are a poor trait to use. But it does illustrate how beautifully genetics can express a disease symptom in an infinitely variable pattern.

FOREST GENETICS WORKSHOP

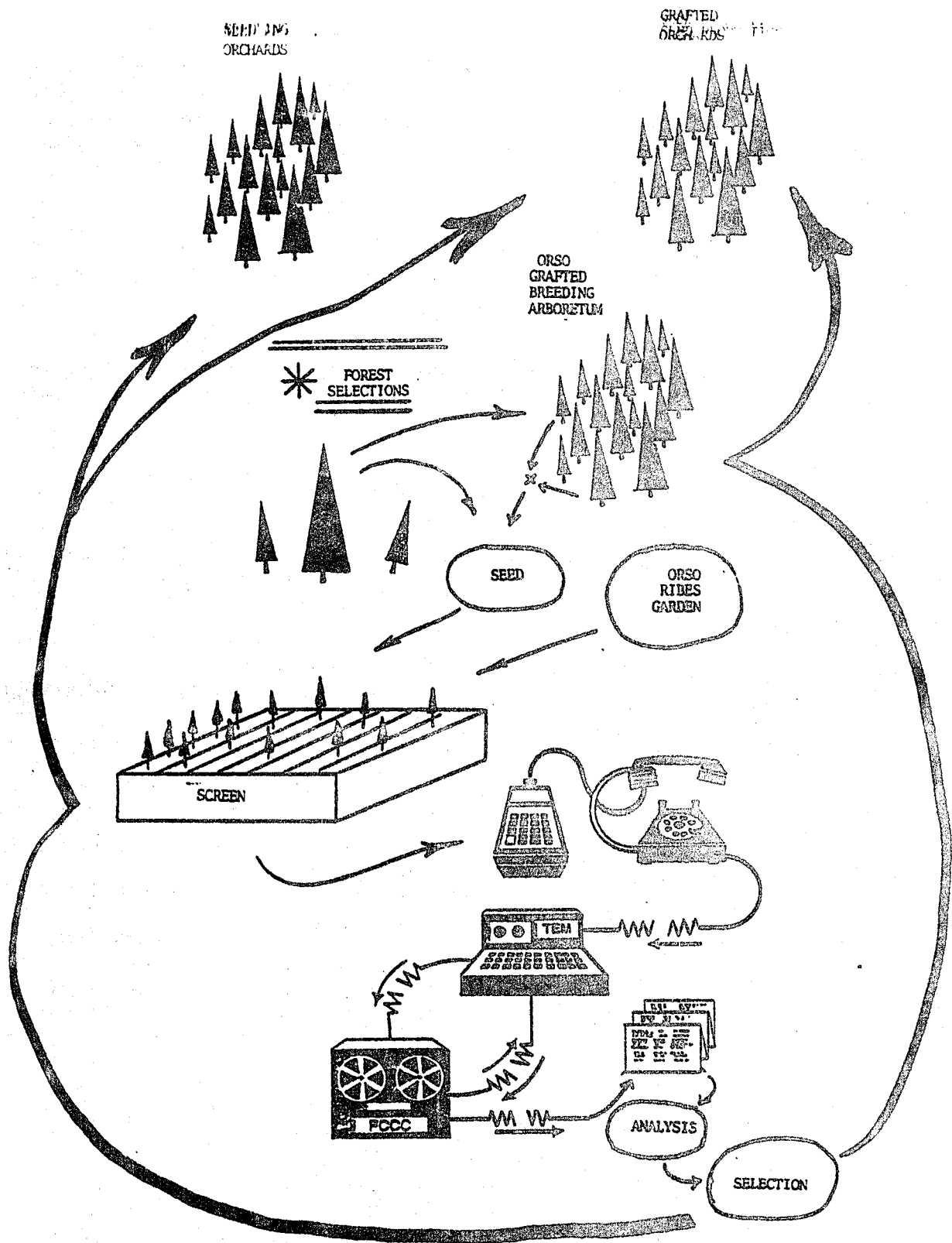
JULY 19 - 23, 1982

EUGENE, OREGON

EASTERN WHITE PINE BLISTER-RUST RESISTANCE  
DEVELOPMENT PROGRAM IN REGION 9

John D. Murphy

EASTERN WHITE PINE BLISTER-RUST RESISTANCE DEVELOPMENT PROGRAM IN REGION 9





## FOREST GENETICS WORKSHOP

JULY 19 - 23, 1982

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### EASTERN WHITE PINE BLISTER-RUST RESISTANCE DEVELOPMENT PROGRAM IN REGION 9

#### OBJECTIVES

In the Lake States, it has been estimated that if resistant stock was available that up to 14 million seedlings would be planted annually. Approximately one million seedlings would be planted annually on the Lake States National Forests if available. These figures prompted the Chief in 1965 to direct the Forest Service to initiate a cooperative effort in the development of a blister-rust resistant eastern white pine seed source. The objectives of the program were to make:

1. Field selections of rust-free phenotypes.
2. Establish a clonal breeding arboretum.
3. Develop and implement a rust screening program.
4. Make control crosses and screen for resistance.
5. Develop, and make available to cooperators, material which could be used for establishing seed orchards.

More recently increased growth rate is being incorporated into the objectives.

#### VALUE OF RESOURCE

The demand for eastern white pine in the Lake States continues to be high due to its excellent wood properties for a great many uses from construction lumber to pulp. On the National Forests, white pine sawtimber value is equal to or greater than red pine, and the volume demand continues to be comparable to other softwood species.

Recently in New York State the screening of various species for resistance to the European strain of scleroderris canker indicated that eastern white pine performed better than red pine. This would make white pine a valuable alternative to some of the millions of red pine seedlings planted annually if this strain of canker became a problem in the Lake States.

#### Organization and Staffing

The National Forest white pine program in the Eastern Region is centered at the Oconto River Seed Orchard on the Nicolet National Forest. Consultation, coordination and program direction is from the Regional Geneticist and Zone Geneticists.

At the Seed Orchard the screening, grafting, and seed production are under the direction of a project geneticist who is directly responsible to the Forest Timber Staff Officer. A full-time technician and several part-time personnel carry-out the various tasks involved in the program.

Each National Forest has one or more technicians or silviculturists who are the prime contacts for carrying-out work at the forest level from selection to evaluation plantation data collection.

#### COOPERATORS

In 1965 a memorandum of understanding was developed and approved by the cooperators listed below with their areas of responsibility.

#### RESPONSIBILITIES

<u>COOPERATORS:</u>	<u>Selections</u>	<u>Scion Collection Control Pollinations On Select Trees</u>	<u>Technical Guidance &amp; Research Records and Basic Research</u>	<u>Coordination Training Orchard Est. Screening</u>
1. USFS-R-9	X	X		X
2. USFS-NCFES			X	
3. UNIV. of WISC.			X	
4. MICH DNR		X		
5. MINN DNR		X		
6. WISC DNR		X		
7. MICH Dept. of Ag.	X			
8. MINN Dept. of Ag.	X			
9. WISC Dept. of Ag.	X			

## TIME SCHEDULES

In the beginning a rather optimistic time schedule was developed as shown in Figure 1. This schedule has been revised and updated as shown in Figure 2. It is expected that some production of limited resistant stock will be available in FY83 and it is hoped that resistance levels and numbers of seedlings will continue to increase over the years.

## SELECTION OF PARENTS

In effect, the Region started off with two sets of selections. The first set consisted of 31 clones tested by Dr. Heimbürger in Canada and 5 selections tested by Dr's. Patton and Riker of the University of Wisconsin. These 36 clones are the basis for an interim seed orchard established in 1969.

The second set of selections consists of over 700 clones which have been selected by cooperators across the Lake States. The selections were made based on the following criteria:

1. Trees growing in a high hazard zone for blister-rust.
2. They had no evidence of present or past blister-rust symptoms.
3. White pine trees adjacent to them were infected with blister-rust.
4. They were between 20 and 60 years of age.
5. They had evidence of flowering.

## ADVANCED GENERATION SELECTION

At the present time advanced generation selection is confined to the selection of young resistant seedlings having gone through the screening process.

## VEGETATIVE PROPAGATION

The grafting for the interim seed orchard and breeding arboretum has been by field units collecting dormant scions from the ortets. These were shipped to the nursery or seed orchard where they were grafted in the greenhouse and moved to a holding area in June. After one or two years the grafts were moved to the field. The initial phase of grafting has essentially been completed at this time.

FIGURE 1 TIME SCHEDULE FOR BLISTER RUST RESISTANT EASTERN WHITE PINE DEVELOPMENT PROGRAM

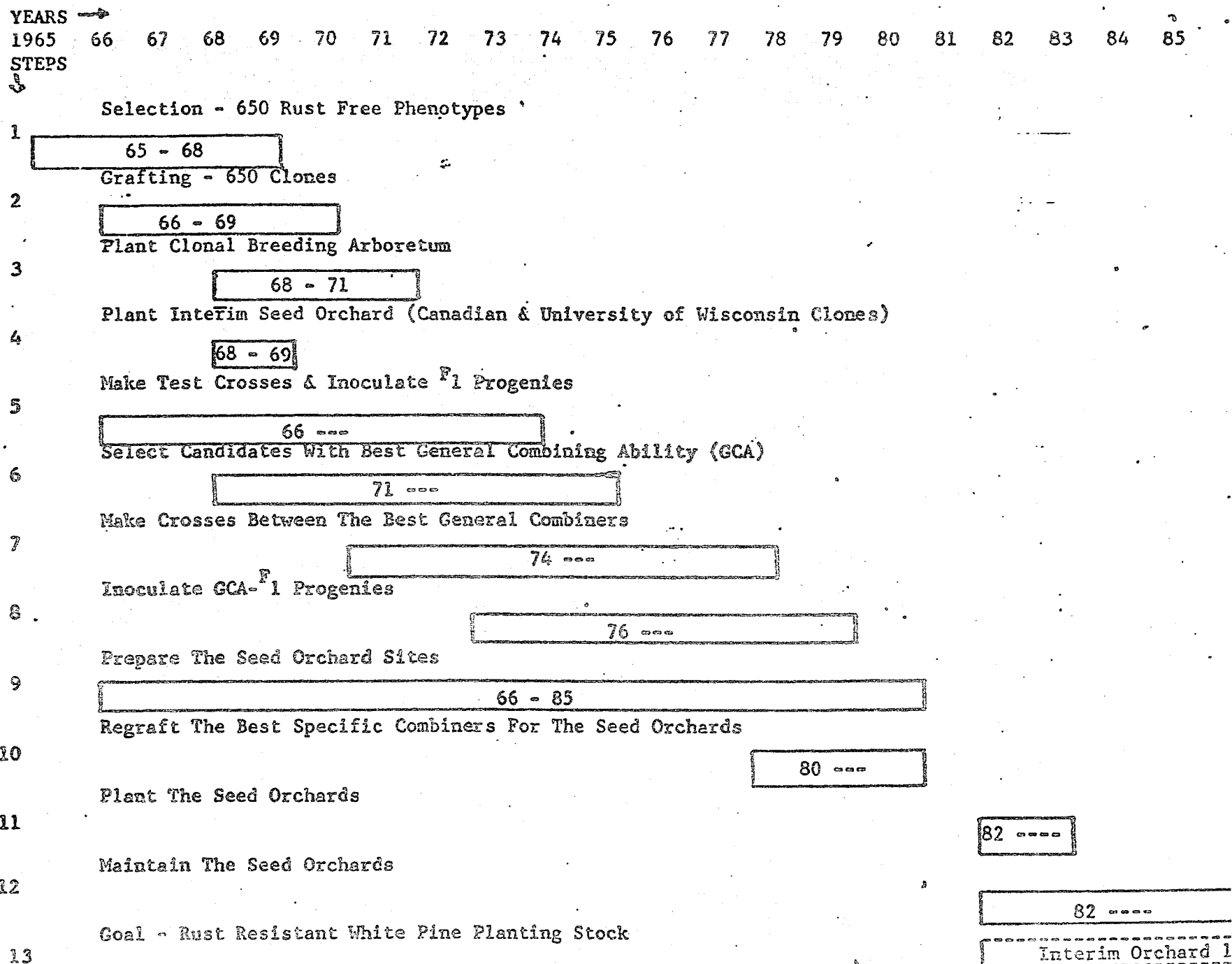


FIGURE 2. REVISED WHITE PINE TIMBER SCHEDULE

R-9 Forest Tree  
Improvement Schedule

Step	Description	8								9								200								201								202								
		0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	
1	Individual Tree Selections																																									
2	Additional Selections as Required	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	
3	Collect Half-Sib Seed (Steps 1 & 2)	WP																																								
4	Propagate Vegetatively (Steps 1 & 2)																																									
5	Establish Seedling Seed Orch. (Step 3)																																									
6	Establish Half-Sib Eval. Plant. (Step 3)					WP	WP																																			
7	Est. Clonal Seed Orch. (Step 4)																																									
8	Est. Clonal Eval. Plant. (Step 4)																																									
9	Rogue Seed Orchards or Eval. Plant. (Steps 5, 6, 7, 8 & 11)																																									
10	Controlled Breeding (Steps 5, 6, 7, 8, & 9)	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	
11	Est. Full-Sib Eval. Plant. (Step 10)																																									
12	Select Individuals in Eval. Plant. (F <sub>1</sub> , F <sub>2</sub> , etc.) (Steps 5, 6, 7, 8, 9, & 11)																																									
13	Est. Advanced Gener. Orch. (Step 12)																																									
14	Controlled Breeding (Steps 12 & 13)																																									
15	Est. Advanced Gener. Full-Sib Eval. Plant. (Step 14)																																									
16	Est. Commercial Plant. with Improved Seed (Steps 3-9, & 11, 13 & 15)	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	WP	

## SEED COLLECTIONS

The production of seed up to this point has been very limited. Seed has been collected from the select trees in the field by climbing or shooting. This seed has primarily been used in the screening process. In some instances quantities of seed have been collected from several trees which were free of rust symptoms and their progeny had done well in initial screenings.

## SEED ORCHARD

At the present time we have one interim seed orchard which consists of 36 grafted clones with a total of 800 ramets. This orchard was established in 1969 and has produced only limited amounts of seed. The best year being after the 1976 drought. As the screening process establishes the data for resistant selections, additional grafted orchards will be established.

## BREEDING ARBORETUMS

The breeding arboretum consists of over 700 clones with 5 ramet row plots. This plantation was initiated in 1969. This planting is on a 20' x 20' spacing. Breeding schemes have been established for the interim seed orchard and the breeding arboretum. This consists primarily of group (priorities) of four disconnected four tree complete diallel, as shown in Fig. 3. This is a recent change from previous schemes consisting of priorities of connected half diallels, which had an unobtainable number of crosses to produce.

## INOCULATION SYSTEM

### Test Facilities:

Our test facilities are located at a 640 acre seed orchard complex on the Nicolet National Forest. A greenhouse is available for producing seedlings. Seed is sown in Ray Leach spruce cells in February. In June the seedlings are transferred to pallets with 10 seedlings from a family in one of the 15 rows with five randomized complete blocks. Pallets are brought into the warehouse for inoculation in August of the second growing season. Only a local source of ribes are used for the inoculation with no attempt to bring in distant aecia spores. Ribes leaves are placed on wire mesh above the pallets and covered with newspaper. Vaporizers are used to maintain a high relative humidity. Microscope slides are randomly placed in the pallets to determine spore cast. When inoculation is complete, the pallets are returned to the outside.

FIGURE 3: TYPICAL PRIORITY FOR WHITE PINE BREEDING SCHEME

Priority 1

	MALE							
FEMALE	0		0				0	
	N	P	N				N	
	4	3	5	0			5	
	9	4	3	N	P	0	0	P
	1	3	8	4	3	N	0	1
					0	2	0	8
ON491	X	X	X	X	X	X	X	X
P343	X	X	X	X	X	X	X	X
ON538	X	X	X	X	X	X	X	X
ON4	X	X	X	X	X	X	X	X
	0			0			0	0
	N	0	P	N			N	N
	6	N	3	4	P	4	4	6
	1	7	2	6	3	7	5	3
	5	0	7	9	2	7	0	8
ON615	X	X	X	X	X	X	X	X
ON70	X	X	X	X	X	X	X	X
P327	X	X	X	X	X	X	X	X
ON469	X	X	X	X	X	X	X	X

### Crew Organization:

The actual screening process is under the direction of the project geneticist. A technician (presently vacant) supervises two to three part-time gardeners involved in producing the seedlings and actual inoculations.

### DATA COLLECTION:

The second growing season, prior to inoculation, a sample of seedlings is evaluated for needle spots. If there appears to be a substantial number of spots then the entire test is evaluated for needle spots from natural infection.

In August of the second growing season the pallets are inoculated. The next June the seedlings are evaluated for survival, needle spot distribution, number of spots, and spot color to include red, yellow, red and yellow, and light green. The status of canker develop and location are also scored. This information is also tallied as a numerical rating for general family scoring and also for use as a history for subsequent data collections. The data codes used are shown in Figure 4.

The next two summers, the scoring is repeated with the exception of needle spots. The surviving seedlings are then moved from the pallet to a field planting.

### EVALUATION OF DATA

The data summaries are used to evaluate which families show the best resistance based on seedling spot status in relation to the percent of seedlings that die from blister-rust, and the percent of seedlings that had spots but have no canker.

### DATA HANDLING AND ANALYSES

Our standard R-9 Tree Improvement Data Handling procedures have been adapted for the blister-rust data collection and processing. All data is collected on electric portable data recorders. It is then transmitted to a terminal and subsequently transmitted to Ft. Collins Computer Center for processing. Our standard summaries are used to summarize the data by family and/or by block. In addition maps of the data can be made for each pallet if desired.

### USE OF TESTED MATERIAL

The material that has been tested is lined out for future use. The data from the test material is used to identify and rate resistance selection which can then be used in developing grafted seed orchards and for additional breeding and testing.



FIGURE 4 CODES USED FOR SCORING INOCULATED SEEDLINGS

1980 Blister Rust Codes for P.D.R.

I-6 Survival

1. Previously Dead - BR
2. This year dead - BR
3. Alive, OK
4. Dead - not BR
5. Permanent vacant

I-12 Needle Spots

- o. No spots
1. Local
2. General

I-10 Spot Intensity

- o. No Spots
1. 1-5
2. 6-25
3. 26-100
4. 100+

I-8 Spot Color

1. None
2. Red
3. Yellow
4. Red & Yellow
8. Light green
- o. Other - Describe

I-9 Canker

1. None
2. Spot - single needle
3. Canker like swelling
4. Bark swelling - orange color
5. Bark swelling - close color
6. Pycnia scars, or aecia, active
7. Pycnia scars, not active, not aecia
8. Appears to be healing
9. Definite canker, in active cork out
- o. Kill canker will or has

I-18 Canker Where

1. None
2. Primary area
3. Stem
4. Lateral
5. Stem and LAT
6. Primary area & Stem & LAT
7. Other

ALPHA	I-21	I-22		Canker Codes
	o1	3o	Dead BR Previously Prim. Area	
	o2	4o	Dead BR Previously - Stem or LAT	
	o3	3o	Dead BR this year primary area	o
	o4		Dead other than BR	
	o5		Permanent vacant	
	o6	4o	Dead BR this year stem or LAT	o
	o7	oo	No spots Year 1 or 2+	
	o8	1o	Spots primary to no canker no canker	
	o9	2o	Spots year 1 primary	
A	11	5o	Spots to spots to canker year 2	
B	12	6o	Spots year 2 (secondary)	
C	13	7o	Spots year 1 Spots year 2	
D	14	8o	Primary area Canker worse	2-7
E	15	8o	Primary area canker worse	o
F	16	9o	Stem or LAT canker worse	2-7
G	17	9o	Stem or LAT canker worse	o
		I-23		
H	18	o1	Canker primary area yr. 1 or 2	2
I	19	o1	Canker primary area Yr 1 or 2	3-5
J	2o	o1	Canker primary area Yr. 1 or 2	6-7
K	21	o2	New canker from spots - Primary	2
L	22	o2	New canker from spots - Primary	3-5
M	23	o2	New canker from spots - Primary	6-7
N	24	o3	New canker from spots - Stem or LAT	2
O	25	o3	New canker from spots - Stem or LAT	3-5
P	26	o3	New canker from spots - Stem or LAT	6-7
Q	27	o4	Old canker No change primary	2-6
R	28	o4	Old canker No change primary	7
S	29	o5	Old canker No change stem or LAT	2-6
T	30	o5	Old canker no change stem or LAT	7
U	31	o6	Needle shed	
V	32	o7	Primary area canker cork out	8
W	33	o7	Primary area canker cork out	9
X	34	o8	Stem or LAT canker cork out	8
Y	35	o8	Stem or LAT canker cork out	9
Z	36	o9	Spots - No canker, No canker	1

## FIELD PLANTATIONS AND EVALUATIONS

Very few acres have been established with improved white pine. In FY 83 about 200M trees will be out planted from the first major collection from our interim seed orchard. Plots will be established in the field plantings for the evaluation of performance for survival, growth and blister-rust status.

## RESEARCH NEEDS

One of the greatest needs for additional research for the screening process is to develop a system for inoculation with a spore suspension. Trials so far have not been successful with blister-rust. There is the continuing need to study the resistance mechanism of white pine and the genetics of the rust as well.

We also must have an integrated research effort to insure that we have the silvicultural knowledge to successfully plant and grow the seedlings after we have resistant material produced.

FUSIFORM RUST RESISTANCE RESEARCH  
AT THE SOUTHERN FOREST EXPERIMENT STATION

Calvin F. Bey<sup>1/</sup>

Abstract

A joint effort of geneticists and pathologists has been directed toward fusiform rust resistance research in Gulfport, Mississippi, spanning the years since this research began in the late 1920's. Current objectives are to improve the selection procedures and to obtain genetic information useful for developing breeding strategies for slash and loblolly pine. Three components of the fusiform rust resistance research are discussed: The importance of geographic and genotypic variation in loblolly pine, the inheritance of resistance, and estimating losses and genetic gain.

Keywords: Geographic variation, breeding strategy, disease losses, genetic gain.

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Fusiform rust resistance research at the Southern Forest Experiment Station had its beginnings around 1926, not long after establishment of the Station (Wakeley 1944). Papers on fusiform rust appeared in the early 1940s (Lamb and Sleeth 1940, Sleeth 1943), and by 1955 a summary paper on control of fusiform rust was published in the Journal of Forestry (Siggers 1955). In the 1955 paper, Siggers points out that geographic differences for fusiform rust resistance exists for loblolly (Pinus taeda L.) but not for slash pine (Pinus elliottii Engelm. var. elliottii). From that early work to the present, scientists at the Southern Station have been involved in many and varied aspects of rust research. Most of the work has been done at the Forestry Sciences Laboratory at Gulfport, Mississippi. This research combines the efforts of geneticists and pathologists. The current objectives in the fusiform rust resistance research are to improve the selection or screening procedures and to obtain genetic information that can be used to develop breeding strategies.

In the past, the Southern Station has worked cooperatively with R-8 in progeny testing for rust resistance. As they screened pine families for resistance they simultaneously obtained some needed research data concerning the screening system. At present, we consider progeny testing, per se, to be a production function and not part of our research mission. The greenhouse aspect of resistance testing is a function of the State and Private Forestry Resistance Screening Center in Asheville, North Carolina, and the field testing is an integral part of the R-8 tree improvement plan.

In the process of improving rust resistance screening methods, we have tested many pine families. Sometimes by design and sometimes fortuitously, we saved seedlings that had resisted infection to establish plantations. Some of these trees are now bearing seed and are available for further research on breeding strategy. Although our new initiatives have concentrated on slash pine, we have also continued our long term studies with loblolly. It is important to remember that there are differences between the species regarding fusiform rust. In terms of resources there are more loblolly than slash planted each year. Of the one million acres planted across the South each year, about 65 percent are loblolly and 35 percent are slash (Abbott and Fitch 1977).

This review will cover three interrelated topics currently under study at the Forestry Sciences Laboratory at Maitland:

1. Geographic variation.--What is the pattern and importance of geographic variation and the genotype x environment interaction in loblolly pine?
2. Breeding strategy.--What are the basic genetic data and how can they be applied in developing breeding strategies?
3. Impact.--What are the yield losses in slash pine due to fusiform rust and potential yield gain through selection for fusiform rust resistance?

A fourth question: "How can we be more effective in our ability in screening for rust resistance?" is an important component of our research and is discussed in the paper, "Progeny Testing the Southern Pines," in these proceedings.

#### Geographic and Genotypic Variation

In general, slash pine and most populations of loblolly pine are both highly susceptible to fusiform rust. Although infection rates may often be comparable, rust associated mortality is less severe in loblolly pine. Some refer to this as rust tolerance in the species. High rates of infection have been attributed to off-site or out-of-range planting, an increase in trees planted, prevalence of the oak alternate hosts, rapid growth due to fertilization, increases in virulence of the pathogen, and climatic conditions. Certain geographic areas are high hazard areas for rust, but predicting infection rates for specific plantations is a risky venture. It's a little like betting on the horses--knowing specific facts can help but there are no sure bets.

Even though resistant slash pine individuals may be more common in some areas than others, they can be found scattered throughout the range (Goddard and Wells 1977). These individuals can be identified by artificial inoculations and/or field testing in high rust areas. Selection efficiency can be increased by selecting in heavily infected plantations and stands (Goddard et al. 1975).

In loblolly pine, geographic variation is distinct and extensive (Wells and Wakeley 1966). Sources near the extremes of the species range--Maryland, Coastal Virginia, Texas, Arkansas, and certain areas in Louisiana and Mississippi--have much greater resistance than the species as a whole, but many of them are relatively slow growing on Coastal Plain sites. Because it combines resistance and good growth, the Livingston Parish (LP), Louisiana, seed source of loblolly pine has been of primary interest over the past 20 years for commercial use of resistant material. Tests established by the North Carolina Tree Improvement Cooperative as late as 1975 confirm many earlier reports of the superiority of the LP seed (Twenty-fifth Annual Report 1981). In the North Carolina Cooperative test the Coastal South LP seed source had about half the fusiform rust infection of local sources. In addition, it outgrew the local sources at eight of the nine plantings in the test. Overall, LP trees were 29 percent taller at age 5 and had 55 percent less fusiform rust (14 vs. 32 percent). It is not surprising that there is still a great demand for LP seed.

To delineate more completely the area of the resistant IP seed, an intensive sampling study was started in 1965 (Wells and Switzer 1971, Wells et al. [in press]). Progeny from 561 parent trees at 113 locations from primarily Louisiana and Mississippi were established at the following three locations: southeast Louisiana, central Mississippi, and northwest Alabama. Fusiform rust infection was examined at ages 4 or 5 and 10. The population west of the Mississippi River, in the loess hills along the east side of the flood plain of the Mississippi River and in the Florida Parishes of Louisiana, was more resistant than sources from the rest of the area. This resistant area is referred to as Zone A. The resistance from Zone A was consistent at all three locations. Many small populations from other areas approached the resistance level of that of Zone A in one planting or another but resistance did not hold up at all locations.

On the average, about one-half of the families from each stand sampled in Zone A were resistant. In contrast, outside of Zone A over 50 percent of the stands sampled had no resistant families at all. The resistant trees from Zone A were consistently resistant at all planting locations whereas only 2.5 percent of those outside of the zone showed consistent resistance. Tree improvers making new selections or additional selections for broadening the genetic base of future generations should find in the Zone A trees a sound opportunity.



## Inheritance of Resistance

It has long been recognized that sufficient genetic variation exists in both slash and loblolly pine to justify breeding for rust resistance. Estimates for inheritance of resistance have generally been moderate to high, and selection programs have identified highly resistant trees. Phenotypic selection combined with progeny testing appears to be the most effective approach for making genetic gains.

Several research studies have shown that fusiform rust resistance is a quantitative trait; that is, it is controlled by many genes (Jewel and Mallette 1967, Kinloch and Stonecypher 1969, Griggs and Walkinshaw 1982). There are no reports of major genes controlling the resistance mechanism. It would be convenient and useful if some early indication could be found as the basis of resistance or at least highly related to resistance. At this stage in our research we are not dealing with a qualitative type of phenomenon, and it is important to emphasize that selection and breeding strategy must be developed and evaluated in a quantitative framework.

A recent study with slash pine in a diallel design shows the need for following the quantitative approach (Griggs and Walkinshaw 1982). Their study involved a crossing of resistant, intermediate, and susceptible trees, followed by inoculation with a composite, virulent, and avirulent isolates of the fungus. With all three fungal isolates, general combining ability for rust galled trees was significant while specific combining ability for the same trait was not. In terms of making genetic gains, this suggests it is not necessary to design crossing programs in orchards with prior knowledge of how specific trees will perform with specific isolates. Gains will be made by selection of parents on the basis of low infection in the progeny and interbreeding of these parents. This corresponds with what is currently being done in slash and loblolly pine improvement work in the South.

Even though we have what appears to be agreement between research results and current practices in tree improvement programs, there is a need for additional research to elucidate some questions concerning the mechanisms of resistance. There are basically two areas that need study. First, there is a serious problem in defining the "type", or "mechanism", of resistance. Secondly, for mechanisms that have been described, there is paucity of genetic statistics on characteristics such as heritabilities, per se. Resistance, as measured by the percent of trees without galls, is the only trait for which useful genetic information exists. Types or mechanisms of resistance generally refer to some refinement of the gall-free condition.

In the literature, types and mechanisms of resistance refer to discernible differences in infection rate, gall morphology, cellular reactions, timing of reactions, and response to diverse fungal isolates. More specifically, they have included inability of the fungus to penetrate the stem; at the cellular level, a physiological reaction to the fungus in the stem; timing of recovery after initial fungal penetration; shape and growth rate differences of active galls; and ability to resist infection over diverse fungal isolates (Kinloch [in press], Griggs and Walkinshaw 1982, Miller et al. 1976). The question of correct classification and assessment as well as clarification of the definition of the actual mechanism, and erroneous implications that sometimes exist is still a problem (Walkinshaw 1978). Once mechanisms are classified, as above, some people assume that families will discretely fit into specific niches. In reality this is not the case and consequently there are scarcely any genetic data on mechanisms per se. More likely, with extensive testing we will likely see a continuum rather than distinct classes. In a sense, every pine genotype would have a different type of reaction, each one with a unique resistance mechanism.

## Estimating Disease Loss and Genetic Gain

Estimating fusiform rust loss in slash and loblolly pine plantations in the South has been a problem--at times even a controversial one. Some people have the opinion that fusiform rust losses are substantial while others feel they are minimal. Often there is no way to resolve these differences of opinion because often they are either not based on scientific data or they are unrealistic assumptions. Holley and Veal (1977) conclude that on an aggregate southwide basis the loss to rust is into the tens of millions of dollars per year, although the estimates have been extremely crude and there is no good basis for judging whether the estimates are liberal or conservative.

We have studied the problem of estimating rust losses. In the process we have come to appreciate that it is important to understand how the loss information is derived and in what manner the loss estimates might be used. Southwide or regional loss estimates are convenient for justifying research, prevention, and protection plans; but they are of no help to the individual forest manager. Foresters want to know how they should manage their lands in the face of the disease. They want to be able to use loss estimates in order to choose among management alternatives. Region-wide disease loss estimates, no matter how precise, will not help a forest manager trying to decide the proper strategy for his 222 acres of slash pine growing on a site where the potential is for 65 feet of growth by age 25, the established density is 930 trees per acre, and 35 percent of the trees have stem galls by age 5. To be useful for management, the potential losses must be based on specific situations. Likewise, accurate estimates of potential region-wide losses are also totally dependent on the specific situations, since accurate region-wide potential loss estimates entail no more than summing individual stand losses.

The reasons for the lack of reliable estimates of fusiform rust losses in forest stands cannot be attributed to the lack of concepts in loss procedures--the concepts were presented by forest pathologist E. P. Meineke in 1928 and have been reiterated and expanded by crop pathologists for many years (Large 1966, James 1974). The reasons for the failure stem primarily from problems inherent in forest trees--they require 20 to 80 years to reach rotation, and disease-loss experiments require control of disease in field plots. Only recently have we had suitable research plots meeting these requirements.

There are two basic approaches to getting loss estimates. The classic approach involves field experimentation using paired plots in which the disease is controlled (Le Clerg 1971). Another approach involves use of data from long-term field experiments that were not originally designed as disease-loss experiments but subsequently became diseased. Where disease and growth are maintained over long periods, these data can, with certain restrictions, offer reliable information on disease-loss relationships. Both approaches are being used by Southern Station scientists to study losses due to rust. We have access to data sets that are suitable for disease-loss estimation and several scientists are in the process of developing and applying these models for specific stand situations. Data suitable for this must meet several standards---it must come from large plots, not rows; it must be long term; and it must have periodic data on density, survival, disease incidence, and tree growth. With data from 187 slash pine plots in Mississippi and Louisiana several important relationships have been investigated: The effect of rust on an infected tree's probability of survival, the modification of this probability due to timing of the infection and the tree's relative competitive status in the stand, and the effect of rust associated mortality on the diameter distribution of survivors. These factors, which affect components in growth and yield models (Dell et al. 1979), were evaluated, and subsequently a growth and yield model was modified (Nance et al. 1981). The modified model permits comparison of infected versus non-infected plots (a loss estimate). Results of this work showed the following:

1. Rust associated mortality was essentially independent of tree size.  
Given equal exposure to the disease, a greater proportion of large than small trees developed stem galls. But survival was higher among large trees than among small trees with stem infections, so that cumulative rust associated mortality was approximately the same in all size classes.
2. Rust associated mortality did not disturb the expected diameter distribution in the plantations, i.e., diameter distributions on plots that suffered rust associated mortality coincided with the diameter distribution expected for non-rust infected plots where the number of surviving trees at age 20 and the site index were the same.
3. The impact of fusiform rust on development of unthinned slash pine plantations can be incorporated into existing growth and yield models by including cumulative rust associated mortality as an independent variable in the survival function. For these data, a modification of Coile and Schumacher's (1964) survival function was developed that provided accurate predictions of survival on both infected and rust-free plots.

Additional growth and yield modeling research with data from an additional 287 plots in Alabama, Florida, Georgia, and South Carolina provided by Union Camp Corporation has shown that essentially the same model can be used for slash pine plantations across the South. In addition, data from a large disease-controlled experiment established in South Mississippi by Froelich and Snow (1977) will add to the model.

Problems associated with estimating genetic gain are analogous to problems of estimating disease losses. Ideally, genetic gains are estimates of increased production based on differences in yield of improved stock over nonimproved stock for a specific management regime such as stocking level, rotation, culture, and prospective utilization. Like disease loss, genetic gain is not a stable or fixed entity. Instead, it is something that varies by management practice and merchantability standard and must be stated in volume (or dollars) per acre to be meaningful. Problems inherent with estimating genetic gain include long rotation and size of the plots. For results to be valid, plots must be large enough to allow inter-tree competition and compensation (within the same genetic unit), similar to typical stand dynamics under plantation conditions. For gain estimation purposes, we have proposed that geneticists examine how improved populations of trees differ from woodsrun populations for traits that are components of growth and yield models (Nance and Bey 1979). In one suitable genetic study Nance and Wells (1981) examined the shape of site index curves and the mean height of trees at index age. Generally the shape of the curve did not vary significantly with the seed source, whereas the mean heights of dominant and codominant trees by source were different at index age. In essence, the genetic aspect of growth was to change the site index component of the growth and yield model. In terms of genetic gains for fusiform rust resistance we can relate back to the research on rust losses. Losses in slash pine are due to decreases in survival from the survival expected in the absence of rust. It is basically the difference in volume between an understocked and a "normal" stand. It follows that genetic gains can be estimated by the increase in survival attributed to rust resistance. Further research is planned in this area using models to estimate genetic gain.

### Summary

Three components of our fusiform rust resistance breeding have been described in general terms. Other aspects of fusiform rust research at the Southern Station include site hazard evaluation, pathogenic variation, histology, and chemical control. Our research demonstrates that gains in rust resistance are possible. Procedures and models for estimating loss and genetic gain have been established.

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Abstract

Heritable resistance of slash and loblolly pine to fusiform rust was demonstrated in wind-pollinated progeny tests of selected trees in the mid 1950's. Since then, additional variation in rust resistance of loblolly pine has been found between stands and among geographic seed sources. Genotype x environment interactions for rust infection either have not been found or have not been of sufficient magnitude to lessen genetic gain from selection of the overall best families. General combining ability for rust resistance is greater than specific combining ability. Seed from wind, or polycross pollination, gives good estimates of rust-resistance breeding values, and artificial inoculation correlates well enough with field infection to provide a technique for early screening of susceptible progeny.

No single breeding strategy is currently in use in the Southeast. First- and second-generation selections are being made and used in clonal orchards with and without progeny testing. Progeny tests may use wind- or control-pollinated seed. Seedling seed orchards are being established from wind- or control-pollinated seed, sometimes with survivors of artificial inoculation trials. Interspecific hybridization of shortleaf x loblolly pine is being used to develop rust-resistant strains of loblolly pine. Two methods not being used are stand selection and nursery selection.

Keywords: Fusiform rust, breeding strategies, selection, hybridization

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In the early 1950's the Southeastern Forest Experiment Station and the Ida Cason Callaway Foundation in west-central Georgia began a cooperative tree improvement program. Trees of all four major southern pines on Callaway lands and in the surrounding area were selected to demonstrate the heritable nature of a number of different traits. One of these traits was resistance or susceptibility to fusiform rust (Cronartium quercuum (Berk.) Miyabe ex Shirai f. sp. fusiforme.). When open-pollinated progeny tests were used, significant differences among families in the amount of fusiform rust infection were evident by 1956 and genetic variations in rust resistance were later confirmed in tests with slash pine (Pinus elliotii Englem.) and loblolly pine (P. taeda L.) (Barber and Reines, 1956; Dorman, 1956; Barber et al., 1957).

In 1953, not long after the work began at Callaway, another series of progeny tests was established. Working out of Macon, Georgia, trees were selected for various combinations of good and poor traits and planted for tests of both wind- and control-pollinated progenies. Early results of three of these tests showed significant differences among slash pine progenies in fusiform rust resistance. Progenies from selected trees averaged 17 percent above commercial check lots (Webb and Barber, 1966). After 10 years, data from two of these tests showed that gains in rust resistance of 36 percent could be obtained by selecting the best 17 percent of the families (Sluder, 1975), which indicated that a relatively low intensity of selection could generate good gains in fusiform rust resistance. The 15-year results of three slash pine tests from these trials also showed great variation among the families (Sluder, 1975). Gains in fusiform rust resistance of approximately 40 percent could be obtained by using the best 36 percent of

the pines tested. By age 15 fusiform rust had taken a heavy toll in these plantations. Total volume losses due to rust mortality, reduced stem growth, and canker tissue were 42 percent for two loblolly pine progeny tests and 55 percent for two slash pine tests (Sluder, 1977).

In 1954 the Georgia Forestry Commission, with guidance from Southeastern Forest Experiment Station personnel, began individual tree selection of slash and loblolly pine for the establishment of first-generation pine seed orchards (Hargreaves and Dorman, 1955). The selection criteria specified that trees must be disease free. Although this requirement was met it could not take into account the possibility that a tree had pruned off branches infected by fusiform rust at an early age. In most cases it has been found that phenotypic selection for rust resistance was not effective. In loblolly pine especially, relatively few first-generation selections have shown better rust resistance than commercial check lots.

The slash and loblolly pine selections made by the Georgia Forestry Commission have been undergoing progeny testing since 1961, mostly as control-pollinated progeny of polymix crosses, some as single crosses, and the last few tests in 1973 used wind-pollinated seed orchard seed. Data from these tests have been used in a number of publications by personnel from the Southeastern Forest Experiment Station.

Fortunately for resistance progeny testing the incidence of the disease is very high in the middle Georgia area. Rust infection in 10- and 15-year old progeny tests commonly is over 80 percent and the average number of rust cankers per tree at age 5 is often three or four. These progeny tests have shown that there are significant differences among slash pine families in resistance to fusiform rust, and that the number of cankers per tree is

a good variable for differentiating among families in young tests before pruning occurs (La Farge and Kraus, 1967). They also showed that genotype x environment (GxE) interactions for rust resistance were not significant for slash pine (Kraus, 1970). Slash pine families that are especially susceptible to fusiform rust become infected even in areas of low rust hazard where many families with only average resistance show no infection at all. Similar results with slash pine progenies were reported by Rockwood and Goddard (1973) who found significant interactions between sites and year planted but a relatively small interaction with the progenies tested. In loblolly pine significant GxE interaction for rust infection has been found (La Farge and Kraus, 1981) but adaptability and stability analyses suggest that the best families are those that maintain a stable superiority in rust resistance over a wide range of rust hazard. Genetic gain was not diminished when the best families were selected in the basis of average performance at all locations, even when there were strong interactions among a few families.

We have also found that polycross progeny are as good as progeny from a single-cross mating design for evaluating the rust-resistance breeding value of selected slash pine (Kraus, 1971). The need to make only one cross instead of four or five, or even to use wind-pollinated seed to evaluate new selections by greenhouse inoculation or by field tests, has been a great help in expanding breeding programs.

Another significant finding from the Georgia Forestry Commission progeny tests was that general combining ability was more important than specific combining ability for slash pine rust resistance, although this difference was not as large as for growth traits (Kraus, 1973). This has important implications for breeding programs. It means that selected progeny-tested

slash pine which has shown good combining ability and high breeding value for fusiform rust resistance but only an average breeding value for growth traits can be crossed with trees having high breeding values for growth traits and average breeding values for rust resistance with some expectation of producing progeny with improved rust resistance. But more important, it means that crossing two trees, each of which has good combining ability and high breeding values for rust resistance, should produce progeny with better rust resistance. For example, in 1974 the Georgia Forestry Commission planted a slash pine seedling seed orchard with 36 progenies of controlled crosses among their best first-generation selections. Fusiform-rust data taken 4 years after planting showed significantly less infection in progenies from crosses with two highly rust-resistant parents than in progenies from crosses in which only one parent was classified as rust resistant. There was a significant but low correlation ( $r = 0.33^*$ ) between the mid-parent breeding values and rust infection of the seedling seed orchard progenies. In an artificial inoculation study of three loblolly pine crosses the percentage of rust infection of the crosses was closely related to the rust resistance of the parent trees which had been determined earlier by using seedlings from wind pollination (Powers and Duncan, 1976). Trees whose wind-pollinated progeny had shown high rust resistance produced even better progeny when crossed with a different tree which had also produced highly rust resistant wind-pollinated progeny.

Breeding strategies for fusiform rust in the southeastern states are also, or should be, influenced by variation among stands. In a wind-pollinated progeny test of 33 loblolly pine (11 trees per stand from each



of three physiographic provinces in Georgia), the genetic variation among stands in percentage of trees rust free was 63 percent greater than that among trees within stands (La Farge, 1974). The great variation among loblolly pine stands in fusiform rust resistance was also shown by the 20th-year results of a geographic variation study begun in 1955. In that study, seed were collected from three stands in each of five physiographic provinces and seedlings planted at two locations in each of the same provinces. After 20 years the variation for fusiform rust was three times greater among stands within provinces than it was between provinces (Sluder, 1980). Although it is difficult to test and then utilize stand variation in a breeding program, the evidence strongly indicates that it is an important factor in fusiform rust resistance.

In state and industry tree improvement programs, the breeding strategy for fusiform rust resistance has changed and become more intense over the years. Initially, most programs used individual tree selection followed by the establishment of clones in grafted seed orchards. Primary traits for selection were high volume growth, good stem form, and high wood density. The selected trees had to be insect and disease free at the time of selection but little or no effort was made to select disease-free trees from heavily infected stands. The effect of this low level of selection in the first generation is evident in a variety trial of slash pine planted in central Georgia. This trial contains seedlings from wind-pollinated bulk collections from 15 state and industry seed orchards. Five years after planting, the most rust-resistant seed orchard lot was only 26 percent rust free (Kraus and La Farge, in press).

About the time that establishment of the earliest seed orchard was completed, concern over losses from fusiform rust infection increased (Kinloch, 1964; Woessner, 1965), and techniques began to be developed for testing

progenies by using artificial inoculation (Goddard et al., 1964). The research on artificial inoculation techniques finally led to the establishment of the Rust Testing Center at Bent Creek, North Carolina which uses a modification of the controlled basidiospore spray (CBS) method developed by Matthews and Rowan (1972). Recent studies have shown good agreement between the amount of rust infection following artificial inoculation and rust infection in field studies, particularly for slash pine (Miller and Powers, 1981; Sluder and Powers 1982). Results from 26 slash pine tests showed that the average rust resistance of progeny from selected trees was less than that of the check lots, but also that some families were much more resistant than average (Schmidt and Goddard, 1971). In loblolly pine, seed orchard clones showed susceptibility to fusiform rust averaging 38 percent infection among 10 clones, with 1 clone as high as 92 percent (Kinloch and Zoerb, 1971). Rust resistance in control-pollinated progeny of these clones was close to the predicted values based on the parent infection in the seed orchard. Further examination of slash pine progeny tests substantiated the fact that little gain in rust resistance could be achieved by phenotypic selection alone, but that good gains would result from progeny testing followed by seed orchard roguing, controlled pollination among parents shown to be rust resistant, or selection of rust-free trees from heavily infected stands, (Rockwood and Goddard, 1973)

That the composition of a seed orchard affects the degree of rust resistance of progeny of a single clone was shown by an artificial inoculation study of five loblolly clones which had been used in several of the North Carolina State University-Industry Cooperative seed orchards. Seedlings of two of the clones tested showed significant differences in rust resistance due to the seed orchard in which the seed were produced (Powers and Zobel, 1978).

The rust-resistance breeding strategies in use today among the state and industry programs are diverse and reflect, in part, the age of the individual programs. Many of the programs, both new and old, are making first-generation selections in natural and planted stands. In most cases these selected trees are not being used in seed orchards until they have been tested at the Rust Testing Center with wind-pollinated progeny from the ortet. The University of Florida-Industry Tree Improvement Cooperative has made 500 new first-generation selections of slash pine. They are evaluating these trees by crossing them with five tester parents from their old orchards. The new selections which produce the most rust-resistant progeny will be used in clonal orchards (R. E. Goddard, personal communication).

Another strategy being used by a few companies is to establish new rust-resistant orchards by using older clones which have already been progeny tested. In some cases, for public relations purposes these are referred to as second-generation orchards but in reality they contain first-generation trees that have undergone two stages of selection. As part of their breeding program, some companies are making diallel crosses among their most rust resistant first-generation selections to generate and establish a population from which they intend to make second-generation selections.

In the cases where true second-generation selection is being done, it too is being used on different levels. Most of the second-generation selection from progeny tests combines family plus individual tree selection. In some cases the select trees are then being used immediately in seed orchards, while in others they are first being progeny tested at the Rust Testing Center before inclusion in clonal orchards. One forest tree seed company plans to cross high volume growth, rust resistant second-generation loblolly

pine selections in a 2 x 2 disconnected factorial mating design. The company hopes to use the best of the resulting progeny to produce rooted cuttings on a commercial scale.

Various types of seedling seed orchards are also being used to increase the production of fusiform rust-resistant seedlings. Buckeye Cellulose Corporation has established one slash pine seedling seed orchard composed of bulked wind-pollinated progenies of 50 first-generation clones, and a second of full-sib crosses of 12 rust-resistant males with 8 rust-resistant females (Rockwood and Goddard, 1973). St. Joe Paper Company also has established a slash pine seedling seed orchard of wind-pollinated progeny from 50 rust-resistant clones. Gains in rust resistance from these orchards are estimated from 8 to 55 percent depending on the parent used, the intensity of rust infection, and the intensity of thinning (Rockwood and Goddard, 1973).

The Georgia Forestry Commission is also using seedling seed orchards as part of their second-generation tree improvement strategy. Since 1973 they have established four slash pine and one loblolly pine seedling seed orchards from progeny of specific crosses of their best first-generation trees. In these orchards they are attempting to combine rust resistance with fast growth and good crown characteristics as shown by earlier progeny tests. The Georgia Forestry Commission in cooperation with the Diseases of Southern Pine Plantations and Seed Orchards and the Tree Improvement work units of the Southeastern Forest Experiment Station is also developing both clonal and seedling seed orchards of slash and loblolly pine to produce highly rust-resistant seedlings (Powers, et al., 1976, 1979). The clonal orchards contain second-generation selections from progeny tests of Georgia Forestry Commission first-generation clones plus rust-resistant selections from other tree improvement cooperatives. The seedling seed orchards are being

established with the survivors of artificial inoculation tests. Estimated gains in rust resistance from these orchards are 50 percent for slash pine and 40 percent for loblolly pine.

Geographic variation in rust resistance is being used by some companies in their planting programs and by a few as part of their tree improvement program. One state has used Livingston Parish, Louisiana, loblolly seed to establish a plantation in a high rust-hazard area. It will be managed like a seedling seed orchard, with frequent roguing of rust-infected, slow-growing trees. One company is using loblolly pine selections from a seed production area in east Texas in making crosses with their selected local loblolly pine.

There is also interest in interspecific hybridization. The  $F_1$  hybrid of P. rigida x P. taeda is highly resistant to fusiform rust. At least one company plans to produce the hybrid for reforestation in high-hazard areas along the eastern coast from South Carolina to Virginia. Similar plans are being made by another company to utilize the high rust resistance of the shortleaf (P. echinata Mill.) x loblolly pine hybrid.

The Tree Improvement work unit of the Southeastern Forest Experiment Station at Macon, Georgia, has an extensive long-term study underway of the shortleaf x loblolly pine hybrid with the ultimate goal of producing a strain of loblolly pine with high fusiform rust resistance based on the genetic resistance of shortleaf pine. The unit found that  $F_2$  hybrids from the Eddy Arboretum at Placerville, California, were completely rust free at two locations in central Georgia (Kraus and La Farge, 1978). Based on this information and an earlier paper by Sluder (1970), the unit began making new  $F_1$ 's with selected shortleaf pine and selected loblolly pine as parents. The Placerville  $F_2$ 's were also used to make backcrosses to selected loblolly pine and to collect  $F_3$ 's from wind pollination. A 5-year-

old field test showed that progeny of selected F<sub>2</sub> hybrids backcrossed to loblolly were significantly more rust resistant than loblolly (1.6 vs 9.0 cankers/tree) but equalled or surpassed the loblolly checks in growth rate (3.5 vs, 3.4 meters). F<sub>1</sub> hybrids and wind-pollinated progenies of the F<sub>2</sub>'s had high levels of rust resistance (0.4 cankers/tree) and were significantly faster growing than the shortleaf check lots (3.1 vs, 2.6 meters) (La Farge and Kraus, 1980).

The susceptibility of F<sub>1</sub>, backcross, and F<sub>3</sub> shortleaf x loblolly hybrids to infection by eastern gall rust (C. quercuum f. sp. echinatae) was tested in an artificial inoculation study. The 18 seed lots tested (6 of each hybrid type) were no more resistant to eastern gall rust than a control seed lot of seed orchard shortleaf pine (Kraus et al., 1982). The same seed lots tested at the same time against fusiform rust basically showed the same high resistance as in our field test.

In another artificial inoculation study, 14 rangewide sources of shortleaf pine were tested with a mixture of fusiform rust spores collected from field-infected backcross hybrids. Infection ranged from 0 to 2 percent, not significantly different from infections by inoculations done at the same time with fusiform rust spores collected from infected loblolly trees used as checks in the same study. So at least in this test, successful infection of hybrids with genes from shortleaf pine has not increased the virulence of fusiform rust to pure shortleaf pine.

In 1978 The Georgia Forestry Commission established a hybrid shortleaf x loblolly seedling seed orchard containing F<sub>1</sub>'s, backcrosses, and F<sub>3</sub>'s from 60 seed lots. Planted on 3 ½ acres at 5- x 8- foot spacing, the orchard will be rogued of fusiform rust infected and slow-growing trees. The seed production from this orchard will be targeted for reforestation of high-

rust-hazard areas. Seed from the best trees plus seed from new crosses will

If anything can be said to stand out in the fusiform rust-resistance programs in the Southeast it is the point that no one is opting for one solution. Almost every state, company, or cooperative is using a multifaceted strategy to increase the fusiform rust resistance of their nursery production. Depending on the age of their program they are using first- or second-generation selection or a combination of both to establish new clonal orchards. Depending upon the theory behind their program they may be using clonal orchards or both clonal and seedling seed orchards. Depending, at least in part, on the severity of fusiform rust in their state or on their lands they may or may not be progeny testing for rust resistance before incorporating a tree in their breeding program.

Possibly the only two techniques receiving little or no use are selection among stands and nursery selection or screening. In the first case there are problems with sampling. How large an area can be defined as a stand? How many trees would need to be sampled? How would yearly variations in male and female flower production on different trees affect the result of a test? If these questions could be resolved, stand seed collections could be tested fairly quickly by artificial inoculation; the fastest growing, best formed trees from which seed were collected in the most rust-resistant stands could then be used in a variety of ways in a breeding program.

In the case of nursery selection or screening, we open a touchy and highly controversial subject fraught with economic and personal biases, my own included, but with very few hard data on record. Fusiform rust is not solely a nursery disease. Therefore, if we protect genetically susceptible

seedlings with Ferbam or Bayleton, the odds are good that they will become infected after planting unless they are planted in a low hazard area. At the same time we may be dispersing genes for rust susceptibility into areas where they did not formerly occur. It may not be entirely coincidence that the increase in fusiform rust damage throughout the South followed the introduction of Fermate as a nursery spray at the same time that thousands of acres were being planted to pine under the soil bank program. Reports of some tests in which fungicides were used in the nursery compare the percentages of infection of the unprotected checks with the sprayed seedlings (Rowan, 1977; Rowan et al., 1980). From these reports it is possible to estimate the percentage of seedlings that have been protected but are rust susceptible. Such estimates indicate that, on the average, approximately 30 percent of the seedlings being shipped are susceptible but have been protected, the range is from 99 percent to 0.1 percent. Some scientists will argue that there are different resistance mechanisms in operation in the nursery and the field, so that seedlings which are resistant in the nursery may not retain their resistance after planting; but this view, at least so far, does not seem valid if we are showing good correlations between rust infection following artificial inoculation of 6-week-old seedlings and rust infection in field trials. Rowan, Cordell, and Affeltranger (1980) estimate the loss from, or extra cost of, producing 30 million rust-free seedlings without spraying in a high-hazard area at \$144,393 per year. They do not estimate the loss from site preparation, planting, and subsequent rust infection on the 55,000 acres that could be planted with that many seedlings.



Unpopular as the idea may be, I think that ecologically and genetically we have no justification for protecting slash and loblolly pine seedlings from fusiform rust infection in the nursery. I would very much like to see additional research conducted to help clarify the consequences of this practice because, if it is as detrimental as I believe, we will have to make some very unpopular recommendations -- recommendations we will have to make as scientists concerned with the long-term benefits to our southern forest and not as pathologists concerned with short-term benefits to the nursery segment of our industry.

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James L. McConnell 2/

The literature on the subject of fusiform rust of southern pines is voluminous. In our files, we have numerous articles dealing with subjects such as: critical reviews, incidence and impact of damage; geographic patterns of fusiform rust infection; incidence and distribution of fusiform rust on different National Forests; evaluations of pathogenic variability; types of resistance and compatibility; fertilizer-induced changes in susceptibility among families; seedling age and fertilization affect susceptibility; pine overstory reduces fusiform rust in underplanted loblolly; early infection as predictors of mortality; and on and on.

Almost all of the writers feel that, and we all know, fusiform rust of southern pines is a major obstacle to the management of slash and loblolly pines.

Even with all of the literature available and the attention given by competent researchers, to me, the picture is still hazy. What's the problem, you might ask? I have talked to District Rangers and Silviculturists throughout the Region and they tell me that rust is not a problem in their area. Until just a few years ago, I was told not to worry about it in our Tree Improvement Program. We no longer take that approach.

Since loblolly and slash pines are two of the major species in our program, we are concerned with fusiform rust. It may not be recognized as a problem on many of our National Forests and, in fact, past management may have made it less severe. I think our long rotations with numerous thinnings tend to lessen the impact on our stands. The current industry practice of growing loblolly and slash pine on pulpwood rotations, with no thinnings or salvage cuts, allows rust to be very damaging. Overall, reduced stocking of plantations due to rust associated mortality is probably the major problem in these stands.

Nevertheless, fusiform rust is here to stay. We must deal with the problem, whatever its severity. One of the most effective ways of dealing with the problem is through the Genetics and Tree Improvement Program.

Within these programs, I think Cal Bey's paper addresses the issue most adequately. After thinking about it for several weeks, there is little left for me to say. The Region's program is attempting to stay current with applied research. Clones in our orchards are being tested at the Rust Screening Center in Asheville. Controlled pollinations are not being tested at the Center because of a lack of seed. We'll have to rely solely on field data from the progeny tests for information on them. Still, I feel, we'll be able to make gains based on the selection of parents from the progeny tests. We'll have to correlate our gains and losses with the management style conducted on National Forest stands. Our management style certainly does not match that of industry in the South, so their data will not directly apply.

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1/ Paper presented at Genetics Workshop, Eugene, Oregon, July 19-22, 1982

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FUSIFORM RUST IN REGION 8, USDA, FOREST SERVICE

Most of the slash and loblolly clones in our present seed orchards have been tested at the Rust Screening Center. We have that information, but right now we don't really know what to do with it. Some clones have tested out very good. The Rust Screening Center test does allow us to drop highly susceptible clones and families from the program.

Until research can get a handle on the "mechanisms" problem, and since many of our National Forests are not in high rust-hazard areas, we may have to adjust our progeny test program. It appears, at present, for our long rotations, a good mix of genetics and silviculture may be the best answer.

THE RESISTANCE SCREENING CENTER -  
SCREENING FOR FUSIFORM RUST RESISTANCE  
AS A SERVICE FOR TREE IMPROVEMENT PROGRAMS

by

Robert L. Anderson  
Supervisory Plant Pathologist  
and Resistance Screening Center Manager

Fusiform rust, caused by the fungus Cronartium quercuum (Berk.) Miyabe ex Shirai f. sp. fusiforme (Cumm.) Burds. et Snow, is considered the most destructive forest disease in the South. The fungus is widely distributed from eastern Maryland to Florida and west to Texas and southern Arkansas. The severity of the disease varies geographically. In some high-hazard areas, it is impossible to grow susceptible trees to harvestable size. Annual losses attributed to the rust are estimated in a 1979 case history report at 600 million cubic feet of southern pine timber, both by degrade and mortality. Using a 1981 blended price of \$0.4031 per cubic foot, this would amount to a loss of slightly over \$241 million in stumpage per year.

Although the disease can be controlled in pine nurseries by fungicides, the use of chemicals to prevent or control the rust in natural or planted stands is not economical. Fortunately, some pines have a natural resistance to fusiform rust. This genetically controlled resistance offers a method to reduce or minimize rust losses. Researchers have identified loblolly and slash pine families that have a high proportion of trees with much more resistance to rust than is found among pines in general. Resistance screening serves to test pine progeny as fast as possible to accelerate the process of identifying resistant parents.

The first resistance screening system used telia-bearing oak leaves suspended over pine seedlings. In the 1970's, the controlled basidiospore suspension (CBS) system was developed by the Forest Service's Southeastern Forest Experiment Station. In this system, pine seedlings are uniformly inoculated using a carefully controlled inoculum density and mechanized spray.

The Resistance Screening Center, which uses the CBS system, was established in 1973 and is operated by the Forest Pest Management Staff of the Forest Service's Southeastern Area, State and Private Forestry. The Center is located at the Bent Creek Experimental Forest near Asheville, N.C. Pine seedlings are evaluated for resistance to fusiform rust as a service to tree improvement specialists, seed orchard managers, scientists, and others in government agencies, research institutions, and private industry. This evaluation enables clients to obtain information on the resistance of their pines in much less time than is possible in field progeny tests. The Center provides information on loblolly and slash pine resistance in eight months; whereas, field progeny tests require 4 or 5 years. By using information from these tests, trees producing rust-resistant progeny are identified.



## The Resistance Screening Center Process:

The screening process is coordinated with the life cycle of the fungus. The life cycle involves two hosts. Aeciospores produced on pines infect only oaks. Basidiospores of the fungus are produced on oaks and infect only pines. Biological materials from both hosts are kept on hand at the Center at all times so that testing can be done year-round. Aeciospores from the fusiform rust fungus are collected and processed for long-term storage each spring. Spores are collected from both loblolly and slash pines in 30 collection areas across the South. In addition, acorns of northern red oak are collected and stored each fall.

The primary steps in the screening process are:

1. Germinate and grow pine seedlings from different seed sources. A seed source may represent an open pollinated family, controlled cross, bulk collection, etc.
2. Inoculate oak host with spores (aeciospores collected from infected pines) to produce a different type of spore (basidiospores), which will infect pines.
3. Harvest spores (basidiospores) from infected oak leaves and prepare spore dilutions of standard density. Critical control and standardization of the inoculum spray is achieved by using an electric particle counter similar to the type used by hospitals to obtain blood cell counts. Without this modification of a medical device, the screening process would be less accurate and more difficult to conduct.
4. Inoculate 6-week-old pines using an automated, mechanical spray system, and incubate at a temperature and humidity optimum for infection. The automated spray system is designed to expose each seedling test to the same amount of inoculum (spores).
5. Evaluate pine seedlings for gall formation after a period of time sufficient for symptom development.

In the standard evaluation, three trays of 20 seedlings from each seedlot are inoculated. The process is then repeated on a second day. At the same time, the Center's own standard check seedlots (usually one resistant and one susceptible) are inoculated for comparison with the client's seedlings. The inoculum (aeciospore) source area is selected by the client according to seed source, planting destination, or other criteria. Modifications of the test design for research purposes may be desirable and can be accommodated within the constraints of the resistance screening process.

## Data Analysis:

Evaluations for fusiform rust resistance provide conservative estimates of the proportion of resistant seed sources. Statistical analysis of the results are included in reports to clients to aid in determining if there are meaningful differences between seed sources. Figure 1 shows an example of the way relative resistance is reported for loblolly pine. In 1981, a new method of ranking slash pine families using an index of relative resistance was

initiated. This system uses the percent and types of galls, as compared to the old system, which only used percent galled. Figure 2 shows an example of how these data are reported. These analyses also provide a measure of the consistency of inoculation procedures and indicate a high level of repeatability.

#### Other Pests:

Forest Pest Management is currently screening National Forest longleaf seedlots to determine their relative resistance to BROWN SPOT. The seedlots are screened using inoculation procedures developed by the Southern Forest Experiment Station. The seedlings are grown under uniform controlled conditions, sprayed with the brown spot fungus, grown for six additional months, and then ranked by percent infection. A southwide screening of slash pine seedlots from selected seed orchards for SEED FUNGI was completed in 1981, and a southwide survey for loblolly is underway. The capability to provide a screening service does exist if funding is available.

Other problems, such as PITCH CANKER, WHITE PINE BLISTER RUST, AIR POLLUTION, and REPRODUCTION WEEVILS, have potential for inclusion in the screening process.

RESISTANCE SCREENING CENTER  
SEEDLOT INFECTION MEANS

Infection Rank	Seedlot	Test Mean	Duncan's Multiple Range on Seedlot Test Means
-	Resistant Check	40	*
1	Seedlot 1	52	*
2	Seedlot 2	54	**
3	Seedlot 3	57	***
3	Seedlot 4	57	***
3	Seedlot 5	57	***
6	Seedlot 6	60	****
7	Seedlot 7	61	***
7	Seedlot 8	61	***
9	Seedlot 9	63	***
10	Seedlot 10	64	***
10	Seedlot 11	64	***
10	Seedlot 12	64	***
-	Susceptible Check	64	***
13	Seedlot 13	65	***
14	Seedlot 14	67	**
15	Seedlot 15	70	*
	All Seedlots	60	

Figure 1.--Statistical analysis of results included in reports to clients for loblolly pine.

RESISTANCE SCREENING CENTER  
INDEX OF RELATIVE RESISTANCE

Seedlot Rank	Seedlot	Seedlot Index
1	Seedlot 1	213
2	Seedlot 2	173
3	Seedlot 3	165
4	Seedlot 4	160
5	Seedlot 5	158
6	Seedlot 6	128
7	Seedlot 7	127
8	Seedlot 8	125
9	Seedlot 9	117
10	Seedlot 10	114
11	Seedlot 11	114
12	Seedlot 12	111
13	Seedlot 13	105
14	Seedlot 14	101
15	Seedlot 15	99
16	Seedlot 16	94
17	Seedlot 17	93
18	Seedlot 18	93
19	Seedlot 19	89
20	Seedlot 20	86
Check	Resistant Check	84
21	Seedlot 21	79
22	Seedlot 22	78
23	Seedlot 23	71
24	Seedlot 24	63
25	Seedlot 25	61
26	Seedlot 26	61
27	Seedlot 27	58
28	Seedlot 28	52
29	Seedlot 29	50
Check	Susceptible Check	47
30	Seedlot 30	37
31	Seedlot 31	37
32	Seedlot 32	23

Figure 2.--Statistical analysis of results included in reports to clients for slash pine.

DESCRIPTION OF  
RUST RESISTANCE MECHANISMS

Dick Miller

One of the objectives of this workshop is to review the blister rust (Cronartium ribicola) and fusiform rust (Cronartium quercuum f. sp. fusiforme) resistance mechanisms that have been identified, and to attempt to develop a common terminology and description for each mechanism.

Prior to the workshop, each Region and Research Station involved with rust-resistance programs was asked to complete a table listing resistance mechanisms by site affected: foliage, bark and undetermined. Hypothesized inheritance, authority and a description were also stated for each mechanism. Data on blister rust resistance mechanisms were received from 4 Regions and 2 Stations. No data were received for fusiform rust mechanisms.

The blister rust data are summarized in Table 1. Ten resistance mechanisms were identified for foliage, 6 for bark and 2 for site undetermined. A review of the data in Table 1 shows that each mechanism has one to several different names and descriptions. This summary was returned to the Regions and Stations for review prior to the workshop.

A copy of Table 1 was given to each attendee at the beginning of the workshop, and was discussed during the field trip at the Dorena Tree Improvement Center. The early discussions centered around whether we were identifying resistance mechanisms or host responses. A consensus was finally reached to use the term "host response." Each response was then discussed. Names and descriptions were agreed upon and are summarized in Table 2. Eleven responses are listed under foliage, 5 under bark, and 2 under site undetermined.

During the workshop, Hoff, McDonald, Powers, Snow, and Kraus discussed the possibility of developing a table identifying host responses for fusiform rust. The host responses shown in Table 3 were developed after much discussion.

The agreed upon names and descriptions (Tables 2&3) will be sent to the Regions, Stations, and State and Private Forestry where disease resistance programs have been initiated. The Washington Office, Timber Management, should be notified when new host responses are identified and if changes need to be made in existing names and/or descriptions.

TABLE 1. RESISTANCE MECHANISMS

MECHANISMS	HOST PATHOGEN	REGION-STATION REPORTING	HYPOTHESIZED INHERITANCE	AUTHORITY	DESCRIPTION
<u>Foliage</u>					
1. Resistance in secondary needles that prevents spot formation. (INT)	WWP/BR EWP/BR	INT R-1 R-5 R-9	Nondominant gene $h^2 = 0.37$	Hoff, Bingham, McDonald, 80	Seedlings do not have needle spots and no stem symptoms. (INT) Failure to produce spots. (R-5)
a. Needle lesions not formed. (R-1)					
b. Reduced needle spot frequency. (R-5)	SP/BR				
2. Reduced frequency of secondary needle infections. (INT)	WWP/BR EWP/BR	INT R-1 R-6 R-9	?	Hoff and McDonald 80	Frequency of needle spots varies with family. (INT) Relatively few spots. (R-1)
a. Low needle lesion frequency. (R-1)			?		Is a horizontal resistance mechanism. Seedlings with this resistance mechanism have 10 times less needle spots than susceptible seedlings. (R-6)
b. Reduced frequency of lesions. (R-6)			Single gene		
3. Resistance in secondary needles to a yellow-spot forming race.	WWP/BR	INT	Recessive gene	McDonald and Hoff, 75	
4. Resistance in secondary needles to a red-spot forming race.	WWP/BR	INT	Dominant gene	McDonald and Hoff, 75	Color of needle spots on seedlings 9 months after inoculation varied. Some were typical lemon-yellow others were bright. The island effect resulted in green-island of needle tissue showing up throughout the red or yellow spot. (INT)
5. Resistance in secondary needles to a yellow-green-island spot forming race.	WWP/BR	INT	Dominant gene	McDonald and Hoff, 75	
6. Resistance in secondary needles to a red-green-island spot forming race.	WWP/BR	INT	Dominant gene	McDonald and Hoff, 75	
7. Premature shedding of infected secondary needles.	WWP/BR EWP/BR	INT R-1 R-6 R-9	Recessive gene	McDonald and Hoff, 70 and 71	Infected needles begin falling off prematurely 9-10 months after inoculation up to 12 months. (INT) Infected needles dropped off. (R-1) The infected needles drop off before the fungus can enter the stem; thus, seedlings with this trait remain healthy. (R-6)
a. Needle shed. (R-1 and R-9)					
b. Spots only. (R-6)					
8. Fungicidal reaction in short shoot. (INT, R-1, and R-6)	WWP/BR	INT R-1 R-6	Recessive gene	McDonald and Hoff, 71	These were seedlings that still had needles with needle spots at 12 months and that did not develop cankers. Appears to be due to an induced toxic chemical. (INT and R-6) Needle spots but no canker subsequently. (R-1)
9. Slow fungus growth in secondary needles. (INT and R-6)	WWP/BR	INT R-6	Polygenic $h^2 = 0.46$		Speed of growth of the fungus down the needle varies by family. Measured by proportion of stem symptoms 1 year after inoculation to stem symptoms 4 years after inoculation. (INT and R-6)
10. Hypersensitivity. (PSW)	SP/BR	PSW R-5	Dominant gene	Kinloch and Comstock, 80 Kinloch and Littlefield, 77	Necrotic lesions. (PSW) Hypersensitive necrotic spots. (R-5)
a. Fleck reaction. (R-5)					

TABLE 1 (Cont.) RESISTANCE MECHANISMS

MECHANISMS	HOST PATHOGEN	REGION-STATION REPORTING	HYPOTHESIZED INHERITANCE	AUTHORITY	DESCRIPTION
<u>Bark</u>					
1. Fungicidal stem reaction. (INT and R-9)	WWP&EWP/BR	INT PSW R-1	Oligogenic $h^2 = 0.37$	Bingham, Squillace, and Wright, 60	Reddish-brown patches show up on the stem following blister rust invasion of the stem. Appears to be due to host tissue necrosis followed by a wound-periderm. (INT)
a. Bark reaction. (R-1)	WWP/BR	R-5		Hoff, Bingham and McDonald, 73	Corking out, callus formation. (R-1)
b. Natural inactivation. (R-1)	WWP/BR	R-6		Kinloch and Byler, 81	The death of apparently healthy cankers. (R-1)
c. Incompatibility. (PSW)	SP/BR	R-9		Bingham, et. al.	Abortive cankers (variable size); non sporulating. (PSW)
d. Bark reaction-incomplete response. (R-5)	SP/BR				Hypersensitive collapsed necrotic canker. (R-5)
e. Bark reaction. (R-6)	WWP&SP/BR				It is a result of the interaction of the fungus and the stem tissue that produces areas of dead host tissues. The fungus is normally slowed down by the necrotic areas. Most often a barrier between infected and healthy host tissues is produced. (R-6)
2. Slow fungus growth in stem. (INT)	WWP/BR	INT R-1	Polygenic $h^2 = 0.21 - 0.46$	McDonald, Hoff and Wycoff, 81	The fungus grows slow enough in the stem so that it does not girdle stem. (INT)
a. Slow canker development. (R-1)	WWP/BR	R-6			A canker which does not girdle the tree, and may lack signs of fungus such as fruiting bodies or orange color. (R-6)
b. Slow fungus growth. (R-6)	WWP&SP/BR				
3. Presence of branch cankers only. (R-1)	WWP/BR	INT R-1	?	Unpublished	Some trees have lots of branch cankers but never (so far) develop cankers on the main stem. (INT)
a. Peripheral canker position. (R-1)		R-5			Branch dies before main stem becomes infected. (INT)
b. Twig blight. (R-5)					Twig dieback ahead of fungal growth in twig. (R-5)
4. Tolerance to infection. (INT and R-6)	WWP&SP/BR	INT R-6	?	Unpublished	Some trees hang on a long time even if severely infected. (INT)
					The canker has occurred at an early stage of growth, but has not girdled the tree, and is not a normal developing canker. It is mostly obvious only through sporulation stage. Seedlings that are cankered but living are propagated and included in the seed orchards in the hope that they can contribute some tolerance to the product from the orchard. (R-6)
5. Hypersensitivity. (PSW)	SP/BR	PSW	Dominant gene	Kinloch and Littlefield, 77	Necrotic lesions (small). (PSW)
6. Reduced infection efficiency. (PSW)	SP/BR	PSW	?	Unpublished	Fewer infections per tree. (PSW)
<u>Site Undetermined</u>					
1. Reduced infection rate. (PSW)	SP/BR	PSW	Polygenic	Kinloch, Byler, 81	Slower rates of infection and mortality over time. (PSW)
2. Ontogenetic resistance. (PSW and R-5)	SP/BR	PSW R-5	Polygenic	Kinloch, Byler, 81	Mature trees less susceptible than offspring--varies by genotype. (PSW)

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TABLE 2. HOST RESPONSE - BLISTER RUST

HOST RESPONSE	HOST PATHOGEN	REGION-STATION REPORTING	HYPOTHESIZED INHERITANCE	AUTHORITY	DESCRIPTION
<u>Foliage</u>					
1. Needle lesions not formed--no spots.	WWP,SP&EWP/BR	INT R-1 R-5 R-9	Nondominant gene $h^2 = 0.37$	Hoff, Bingham, McDonald, 80	Seedlings do not have needle spots and no stem symptoms.
2. Hypersensitivity.	SP/BR	PSW R-5	Dominant gene	Kinloch and Comstock, 80 Kinloch and Littlefield, 77	Spots become necrotic, fungus is arrested.
3. Reduced needle lesion frequency.	WWP&EWP/BR	INT R-1 R-6 R-9	?	Hoff and McDonald, 80	Frequency of needle spots varies with family. Seedlings with this response have less needle spots than susceptible seedlings. Threshold levels should be based on spots per spore.
4. Resistance in secondary needles to a yellow-spot forming race.	WWP/BR	INT	Recessive gene	Hoff and McDonald, 75	
5. Resistance in secondary needles to a red-spot forming race.	WWP/BR	INT	Dominant gene	Hoff and McDonald, 75	Color of needle spots on seedlings 9 months after inoculation varied. Some were typical lemon-yellow others were bright. The island effect resulted in green-island of needle tissue showing up throughout the red or yellow spot.
6. Resistance in secondary needles to a yellow-green-island spot forming race.	WWP/BR	INT	Dominant gene	Hoff and McDonald, 75	
7. Resistance in secondary needles to a red-green-island spot forming race.	WWP/BR	INT	Dominant gene	Hoff and McDonald, 75	
8. Premature needle shed.	WWP&EWP/BR	INT R-1 R-6 R-9	Recessive gene	McDonald and Hoff, 70 and 71	Premature needle shed of secondary needles. The infected needles drop off before the fungus can enter the main stem.
9. Fungicidal reaction in short shoot.	WWP/BR	INT R-1 R-6	Recessive gene	McDonald and Hoff, 71	Seedlings that have needles with needle spots at 12 months that did not develop cankers.
10. Spots only.	WWP/BR	INT R-1 R-6	?		Combination of 8 and 9.
11. Slow fungus growth in secondary needles.	WWP/BR	INT R-6	Polygenic $h^2 = 0.46$		Speed of fungus growth down the needle varies by family. Measured by proportion of stem symptoms 1 year after inoculation to stem symptoms 4 years after inoculation.



TABLE 2 (Cont.) HOST RESPONSE - BLISTER RUST

HOST RESPONSE	HOST PATHOGEN	REGION-STATION REPORTING	HYPOTHESIZED INHERITANCE	AUTHORITY	DESCRIPTION
<u>Bark</u>					
1. Bark Reaction.	WNP, EWP&SP/BR	INT PSW R-1 R-5 R-6 R-9	Oligogenic $h^2 = 0.37$	Bingham, Squillace, and Wright, 60  Hoff, Bingham, and McDonald, 73 Kinloch and Byler, 81, Bingham et. al.	A result of the interaction of the fungus and the stem tissue that produces areas of dead host tissues. The fungus is normally slowed down or inactivated by the necrotic areas. The necrotic areas vary from very small at base of needle fascicle to large when girdling stem.
2. Slow fungus growth in stem.	WNP&SP/BR	INT R-1 R-6	Polygenic $h^2 = 0.21 - 0.46$	McDonald, Hoff and Wycoff, 81	A canker which does not girdle the tree, and may lack signs of fungus such as fruiting bodies.
3. Presence of branch cankers only.	WNP&SP/BR	INT R-1 R-5	?	Unpublished	Branch dies before main stem becomes infected.
4. Tolerance to infection.	WNP&SP/BR	INT R-6	?	Unpublished	Cankers have occurred at an early stage of growth, but have not girdled the tree, and are not normally developing cankers. They are mostly obvious only through sporulation stage.
5. Reduced infection efficiency.	SP/BR	PSW	?	Unpublished	Fewer infections per tree.
<u>Site Undetermined</u>					
1. Reduced infection rate.	SP/BR	PSW	Polygenic	Kinloch, Byler, 81	Slower rates of infection and mortality over time.
2. Ontogenetic resistance.	SP/BR	PSW R-5	Polygenic	Kinloch, Byler, 81	Mature trees less susceptible than offspring--varies by genotype.

TABLE 3

## HOST RESPONSE - FUSIFORM RUST

RESPONSE	HYPOTHESIZED INHERITANCE	AUTHORITY	DESCRIPTION
No galls.	Family related	Snow and Powers	No stem infections with no purple spots on stem.
Early Cortical Reactions. (Multiple Response)	Family related	Snow, Miller, Jewell, and Walkinshaw	Purple spots to purple blotches on stem that do not become galls.
Recovery from stem infections.	Family related	Snow and Powers	Necrosis within cankers that result in disappearance of gall. Small to large amounts of necrosis. The infection heals over.
Reduced size of galls.	Family related	Snow and Powers	Small stem infections (pinhead size to 4-5 inches in length).
Constricted galls.	Family related	Snow and Powers	Globose galls. Galls with "collars."
Number of galls.	Family related	Powers and Snow	Fewer galls per individuals and families.
Phenological escape.	Family related	Froelich, Snow, and Lewis	Infection tissue is out of phase with inoculum load.

Pathogenic Variation Within Cronartium quercuum f. sp. fusiforme

by

H. R. Powers, Jr.<sup>1/</sup>

ABSTRACT

The Cronartium quercuum complex includes four formae speciales on eastern and southern hard pines; some have been shown to be highly variable in pathogenicity. The fusiform rust organism, on loblolly and slash pines, has been most extensively studied. Results of these studies indicate differences among rust isolates from single galls, from different galls within an area, and from galls collected in different geographic areas. The level of pathogenicity varies with pine family, and there are interactions between rust isolates and pine families.

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Many studies have shown extreme variation in pathogenicity of Cronartium rust organisms. It is tempting to relate the host-pathogen situation in tree rusts to that of cereal rusts because so much information is available on cereal rusts (2, 3). The concept of physiologic races of rusts was established for the black stem rust of wheat, caused by Puccinia graminis tritici (16). In this paper, I review the situation regarding the Cronartium quercuum complex in the Eastern United States, and also present some comparisons with the cereal rusts and their nomenclature on pathogenic variability.

The first reports of variability within the Cronartium quercuum complex came in papers presented by Kais and Snow (4), and by Powers (5) during a 1969 rust symposium. The two studies independently yielded the same conclusion: there

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are distinct differences between the isolates of Cronartium quercuum collected from jack, Virginia and shortleaf pines, as well as differences between other isolates. The key finding was that an isolate from Virginia pine could infect its own host species but not jack pine, and that jack pine isolates could infect jack pine, but not Virginia pine. In other words, the classic interaction between hosts and rust isolates that led to the differentiation of "physiologic races" within the stem rust of cereals complex was present. Both papers referred to this phenomenon as indicating racial variation within Cronartium quercuum.

Later Burdsall and Snow (1) dealt with the entire Cronartium quercuum complex. They constructed a system of formae speciales with Cronartium quercuum f. sp. banksianae on jack pine, f. sp. virginianae on Virginia pine, f. sp. echinatae on shortleaf pine, and f. sp. fusiforme on loblolly and slash pines. In other words, these formae speciales were based on differences between species within the genus Pinus. In contrast, the formae speciales of cereal rusts are based on differences between host genera (Puccinia graminis tritici on wheat, P. graminis secalis on rye, etc.). The cereal rust formae speciales are then subdivided into physiologic races based on their pathogenicity. In the case of wheat, 12 varieties are inoculated to identify the fungal race. Race is determined largely from the quantitative production of urediospores on the wheat varieties. An important point here is that the 12 differential varieties fall among five distinct species of genus Triticum.

Burdsall and Snow's nomenclature has been well accepted by most workers on the rusts of eastern and southern pines. The system provides discrete differences that can be easily utilized. They also suggested the term "pathotype" rather than "race" for the secondary variability within a formae speciales. This convention seems reasonable because there are inherent differences between the Cronartium rusts and

the cereal stem rust complex. First of all, the disease types in stem rust are based on quantitative differences while ours are qualitative. We measure the percentage of inoculated seedlings with fusiform rust galls after a given period of time, while cereal pathologists observe production of urediospores. Some types of fusiform rust symptoms have recently been better defined, and these results will help to clarify the type and source of variation. In addition to these differences, the spores doing most damage on cereals are the urediospores, the repeating stage of the life cycle. These spores form what are essentially clonal lines, and can exist from year to year without going through the sexual stage. With the Cronartium rusts, the spores infecting the economically important pine hosts are basidiospores, the product of sexual recombination and meiosis. Therefore, there is a much lower possibility of genetically similar "races" or "pathotypes" developing. Nevertheless, there are very sharp differences in pathogenicity at every level studied in the C. quercuum complex.

Most of the work on pathogenic variation in this complex has dealt with C. quercuum f. sp. fusiforme, the fusiform rust organism. Evidence of pathogenic variation within the fusiform rust organism was provided by Snow and his co-workers in 1970 (14). They found significant differences between slash and loblolly pines inoculated with the fusiform rust organism from five sources in the Southern United States. Subsequent work by Snow with 10 slash pine families indicated significant rust inoculum x family interactions, and demonstrated substantial differences in resistance among families and in pathogenic variability among rust isolates (13). On one resistant family, active galls were completely absent after inoculation with two rust isolates. This was the first observation of an immune reaction between the fusiform rust organism and slash pine. In addition, two of the families were resistant to all of the inocula with which they were tested. This phenomenon was interpreted as similar to horizontal resistance which has been observed in various agronomic crops.

This work was followed by an extensive sampling of the population of the fusiform rust organism on loblolly pine across the Southern United States (10). Collections from 26 individual galls from seven states (Louisiana through North Carolina) were used to inoculate three loblolly pine families rated as resistant, intermediate, and susceptible to fusiform rust. Highly significant variation was found among pine host families, and among rust collections from different states. Significant interactions between families and rust collections were also observed. Even the most resistant family (11-20) was highly susceptible to infection by one of the single gall rust collections. There was also as much variation between some individual rust collections from within a single, localized areas as there was among collections from different states. This have been found to be true in both slash and loblolly pine.

The work with loblolly also provided evidence of the classic reversal of infection types on two families, similar to the differential reactions on wheat that result in the classification of physiological races. That is, one family is susceptible to one isolate but resistant to a second, while a second family exhibits the reverse response. These could be labeled "pathotypes", since some effort should be made to identify these strains and use them to test resistant pine clones.

Additional research on the interactions between specific loblolly pine families and virulent rust collections was carried out with nine families ranging from resistant to susceptible, and five rust isolates (8). These results are shown in Table 1. All families rated as resistant had relatively low levels of infection, but only one was resistant to all isolates. Family 11-20 was resistant to four isolates, but as mentioned earlier, quite susceptible to the rust collection from its own native area. The Texas selections were quite resistant to most isolates, but again much more susceptible to the rust originating from their own state. The

same was true for a selection from Livingston Parish, Louisiana. There appears to be a clear tendency for pines from a specific area to be susceptible to the rust from their native geographic area.

The possibility of the rust fungi developing increased virulence on resistant pine selections is a matter of great concern to both geneticists and pathologists. One resistant slash pine family tested by Snow and his co-workers (15) provide a dramatic example. Collections of fusiform rust from field-infected members of this pine family caused infection of 77% of exposed seedlings of this same family. The infection rate from exposure to the general rust population was only 17%. Such sharp increases in virulence are obviously a direct challenge to programs of selecting and breeding for resistance. Additional studies on loblolly pine have also indicated increases in virulence, but not of the magnitude observed in slash pine (11). Three families of loblolly pine, a resistant family from which the rust collections were made, an unrelated resistant family, and a susceptible check were studied. Rust collections were from field plantings of the resistant family, and from the general rust population in the same area. These results indicated no statistical difference in virulence between the two groups of rust collections. However, there was a 9% increase in virulence. This may be biologically important even if not statistically significant. Another interesting point was that there was no increase in virulence on the non-related, rust resistant family.

Other research has been done to determine if a trend toward higher levels of virulence was developing in recent years (7). Rust populations from galls originating approximately in 1945 were compared with those originating about 1970. The results showed no difference in virulence between the two groups, but it was obvious that the more recent collections were much more variable.

One recent study extends the work on pathogenic variation within the fusiform rust organism one additional step (6). In this study aeciospores were collected

from one isolated rust gall and used to establish 10 single-spore rust collections. These collections were used to inoculate resistant, intermediate, and susceptible families of pine. The results showed highly significant differences among the mean infection levels produced by these single spore collections.

Another interesting point with regard to fusiform rust on loblolly pine is that there are specific geographic areas, primarily around the periphery of the natural range of this species, which provide reasonable levels of resistance. These areas are: Arkansas, Texas, Louisiana, Maryland, and Florida. In an additional study seedlings from these areas were inoculated with rust collections from each area involved (9). The results are shown in Table 2. The Maryland seed source was most resistant. There were also highly significant interactions between seed sources and rust collections from different geographic areas. In all cases, the infection level on a specific seed source was highest when it was inoculated with rust spores from the same area. There seems to be a trend for virulence to develop where the complementary genes for resistance are found.

It is safe to say that C. quercuum f. sp. fusiforme shows a wide range in virulence on all of the hosts that have been studied. We do not, however, expect a situation to develop comparable to that of the cereal rusts, in which there is a shifting of pathogenic races on almost a yearly basis. However, we can certainly expect changes in pathogenicity among forest tree rust pathogens. We, therefore, should constantly monitor the relative pathogenicity of these fungi, particularly in areas where large-scale plantings have been made with a specific source of resistance. Early warnings from such studies would enable us to change patterns of deployment of our resistant materials, and to stay at least one step ahead of the pathogen in the race to maintain effective disease control.



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TABLE 1. Infection produced on nine loblolly pine families inoculated with five isolates of Cronarium quercuum f. sp. fusiforme

Pine family and state of origin	Rust isolate and percent seedlings infected					Host mean
10-5 (GA)	GA (30) <sup>y</sup>	MS (34)	TX (35)	SC (39)	LA (41)	36a <sup>z</sup>
11-20 (SC)	GA (34)	LA (38)	TX (39)	MS (43)	SC (71)	45b
B-5-4 (LA)	SC (29)	GA (38)	MS (39)	TX (48)	LA (76)	64b
S-6-5 (TX)	GA (33)	<u>SC (40)</u>	<u>MS (43)</u>	<u>LA (58)</u>	TX (65)	48b
S-4-8 (TX)	<u>SC (43)</u>	<u>GA (46)</u>	MS (58)	<u>TX (63)</u>	LA (65)	55c
7-56 (SC)	<u>TX (48)</u>	<u>LA (61)</u>	<u>MS (64)</u>	<u>SC (65)</u>	GA (68)	61d
15-42 (GA)	<u>TX (45)</u>	<u>SC (46)</u>	<u>MS (65)</u>	<u>GA (78)</u>	LA (88)	64d
4-R (GA)	<u>SC (80)</u>	<u>GA (80)</u>	<u>LA (81)</u>	<u>MS (83)</u>	TX (84)	82e
3838-3 (GA)	<u>MS (75)</u>	<u>GA (78)</u>	<u>LA (83)</u>	TX (91)	SC (92)	84e

<sup>y</sup>Numbers in parentheses are percent seedlings infected.

Means underscored by a common line do not differ significantly according to Duncan's multiple range test, P = 0.05.

<sup>z</sup>Host means followed by the same letter do not differ significantly at the P=0.01 level as determined by Duncan's multiple range test. Each mean, however, should be evaluated by state since there was a significant family X isolate interaction.

TABLE 2. Incidence of infection on seedlings of six geographic sources of loblolly pine after inoculation with rust fungus collections from each geographic area

Seed sources	Seedlings (%) with galls 9 mo. after inoculation with spores from:						Host mean
	GA	MD	AK	FL	TX	LA	
Maryland	53	<u>69</u> <sup>y</sup>	49	52	56	55	56a <sup>z</sup>
Arkansas	54	48	<u>72</u>	61	68	61	61b
Florida	69	74	49	<u>76</u>	61	73	67c
Texas	58	53	80	68	<u>84</u>	83	71c
Louisiana	78	73	81	81	81	<u>82</u>	79d
Georgia (control)	<u>88</u>	89	81	82	80	87	84e
Mean	66a	68ab	69abc	70abc	72bc	73c	(70)

<sup>y</sup>Underlined figures indicate the incidence of infection in trees inoculated with a local source of the rust fungus.

<sup>z</sup>Infection percentages followed by the same letter do not differ significantly ( $P=0.01$  for host means and  $P=0.05$  for spore means) as determined by Duncan's multiple range test.

# GENETICS OF CRONARTIUM RIBICOLA

by

G. I. McDonald

I want to begin this presentation with a statement by R. G. Grogan (Horsfall and Cowling 1980) that embodies my philosophy about racial variation in plant pests: "If you find an organism misbehaving in the field, don't spray it, don't fumigate it, investigate it!" The essence of this statement is that phenotypic variation is the key to genetic understanding, and genetic understanding is the key to successful pest management. Our approach to the study of variation in C. ribicola has been to investigate any observed misbehavior and even to seek or create misbehavior in attempts to uncover a trait or traits that will facilitate genetic study. So far, we have investigated four areas of misbehavior: (1) needle spot color morphs, (McDonald and Hoff 1975; McDonald 1978); (2) genetic variation of epidemiologic fitness traits (McDonald and Andrews, in press); (3) characterization of a canker explosion on "resistant" trees (McDonald, Hansen, Osterhouse and Saman in preparation); and (4) geographic variation of aeciospore infection efficiency on ribes leaves (McDonald unpublished data).

## Needle spot color

In 1964, we noted the presence of red needle spots in an ongoing progeny test at Moscow. In 1967, we recorded incidence and collected samples for histological study of various needle spot types. A paper

was ultimately published (McDonald and Hoff 1975) that outlined a hypothesis of rust pine interaction. Three facts pointed toward a specific genetic or racial interaction. First, the infected pine seedlings seemed to be composed of three kinds: red-spots-only; yellow-spots-only; and both red and yellow. Second, there was a frequent occurrence of red and yellow spots in juxtaposition on the same needle which argues for genetic variation of the rust as the cause of the morphologic variation. Third, the frequencies of infection on the three classes of plants acted as though the single-type plants were resistant to the non-occurring types and that the double-type plants were susceptible to both spot-color races.

These ideas were tested by collecting aeciospores from the three infection-spot-type seedlings and producing basidiospores for inoculation back to pine (McDonald 1978). These results did not fit the hypothesis exactly, but they did show a strong association with the parental spot type. Red-only produced 79% red-only aeciospores; all plant types produced about 12% mixed aeciospores, and the yellow-only types produced 56% yellow-only. These results highlighted that the genetics of Cronartium ribicola is little understood.

### Epidemiologic fitness

Our next major area of genetic investigation of C. ribicola was quantitative genetic analysis of epidemiologic fitness traits. Four traits (Fig. 1) were studied in single aeciospore populations from a group of individual blisters. If assumptions are made that all aeciospores from a single blister result from one fertilization event, then we have a way to compute minimum values for proportion of variation due to genetic factors. All traits studied seem to be under fairly strong genetic control (Fig. 1).

These studies also resulted in a suggested method for conducting a full-scale factorial mating to meet all the assumptions of a diploid population (Fig. 2) thus making it possible to compute narrow sense heritabilities and maternal influences for any measurable rust trait.

### Geographic variation

Since aeciospores can travel long distances (up to 400 miles), and pine material may be moved extensively in the future, we deemed it desirable to investigate geographic variation of the rust. The initial study was conducted during the spring of 1982. Five ribes bushes of each of four species of ribes plants we collected at four areas in late summer of 1981. Two areas were located in northern Idaho (Merry Creek

QUANTITATIVE GENETIC ANALYSIS  
OF C. RIBICOLA

TRAIT	$\% V_t$ DUE TO $V_g$
ASPORE CULT. GROWTH RATE	33
EARLY Tspore FORMATION	30
UREDIAL PUSTULE DENSITY	38
UREDIOspore INOCULATION SUCCESS	17

Figure 1. Amount of genetic variation in a population of single Cronartium ribicola aeciospores shown by quantitative genetic analysis assuming fertilization event per aecial blister



QUANTITATIVE GENETICS OF C. RIBICOLA  
PROPOSED FACTORIAL MATING

♀ SINGLE ASPORE (PYCNIA)	♂ SINGLE ASPORE (PYCNIOSPORES)	
	A	B
1	1-1 X A-1	1-5 X B-1
	1-2 X A-2	1-6 X B-2
	1-3 X A-3	1-7 X B-3
	1-4 X A-4	1-8 X B-4
2	2-1 X A-5	2-5 X B-5
	2-2 X A-6	2-6 X B-6
	2-3 X A-7	2-7 X B-7
	2-4 X A-8	2-8 X B-8

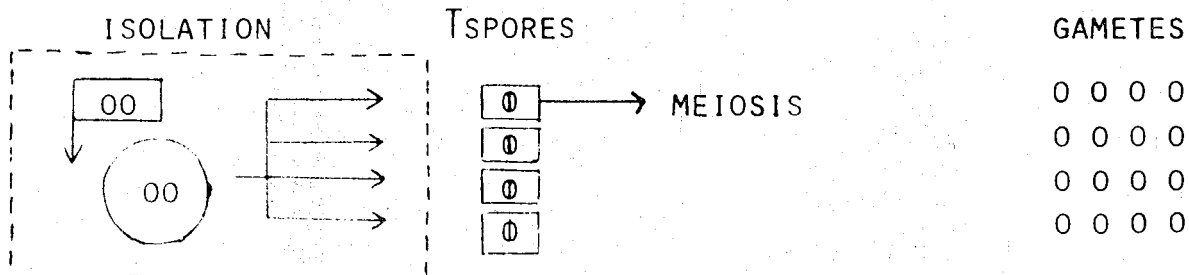


Figure 2. Proposed study of *Cronartium ribicola* to obtain factorial mating that would create a population satisfying all quantitative genetic assumption applicable to a diploid population.

and Priest River Experimental Forest); two were located in the Oregon Cascades (Champion Mine and Hill Creek). Aeciospores were collected in May of 1982 at the four areas and then transported back to Moscow for inoculation to the ribes plants. Inoculation was conducted on detached leaf discs in replications. The inoculated discs were then inspected daily from the 6th to the 21st day after inoculation. The initial results show much variation associated with aeciospore source and some with ribes bush source in the case of both R. lacustre and R. bracteosum (Fig. 3). In general, for both ribes species, northern Idaho sources of aeciospores produced more infection than the Oregon sources. Most noticeable was the low amount of infection caused by the Champion source. These data are a summary of about one-fourth of the data collected for the geographic variation study; so, these results are presented only to show direction of research and trends in the data.

Also, within the geographic variation data were records of individual bush performance (Fig. 4). The pattern is rather typical of results for all species except for clone 2. We have no other immune clones. There is some evidence for ribes clone x aeciospore source interaction. These results show hope for finding and isolating some individual aeciospore x clone virulent-avirulent reactions for use as genetic markers. They also point toward the possibility of making field selections for increased resistance in Ribes hudsonianum. Other species of ribes (R. lacustre, R. bracteosum, R. sanguineum, and R. viscosissimum) showed the same trend.

RIBES -- RUST GEOGRAPHIC VARIATION  
INFECTIONS/CM<sup>2</sup>

RIBES LACUSTRE

RIBES SOURCE	AECIOSPORE SOURCE				$\bar{x}$
	CHAMPION	STILL	MERRY	PRIEST	
CHAMPION	3.64	6.36	14.68	9.74	8.61
STILL	4.16	10.26	13.18	15.65	10.81
PRIEST	3.64	7.73	12.60	12.92	9.22
	3.81	8.12	13.49	12.77	9.55

	<u>RIBES BRACTEOSUM</u>				$\bar{x}$
	CHAMPION	STILL	MERRY	PRIEST	
CHAMPION	4.87	10.45	12.88	16.63	11.21
STILL	8.12	12.01	14.68	25.49	15.08
	6.50	11.23	13.78	21.06	13.15

Figure 3. Patterns of geographic variation after artificial inoculation of 2 *Ribes* species from 3 locations with *Cronartium ribicola* aeciospores from 4 areas.

RIBES -- RUST GEOGRAPHIC VARIATION

INFECTIONS/CM<sup>2</sup>

RIBES HUDSONIANUM INDIVIDUAL BUSHES

RIBES H. CLONE	AECIOSPORE SOURCE				$\bar{X}$
	CHAMPION	STILL	MERRY	PRIEST	
1	4.35	5.76	20.04	21.29	12.86
2	0.0	0.0	0.0	0.0	0.0
5	10.44	19.16	21.13	15.42	13.93
7	.27	1.30	.97	.10	.66
8	.54	4.23	5.90	1.84	3.13
	3.12	6.09	9.61	7.73	6.12

Figure 4. Patterns of individual bush infection levels within a population of Ribes hudsonianum inoculated with Cronartium ribicola from 4 locations.

## Canker explosion

During the early 70's, a rapid increase took place in the canker population on a group of phenotypically resistant western white pine growing on an isolated high elevation site (Champion Mine) in the central Oregon Cascade mountains. At the same time, a striking decrease of numbers of resistant seedlings obtained from progeny tests at the Dorena Center was observed when inoculum from the site was used. A study was initiated in 1977 to investigate these progeny test observations in a controlled experiment (McDonald, Hansen, Osterhouse and Saman, in preparation). The experiment consisted of two pine populations RCP (resistant controlled pollinated) composed of plants from Champion Mine parents which had been selected for resistance prior to 1970 and UOP (untested open pollinated) composed of plants from phenotypically resistant trees that were in current progeny tests. The rust inoculum was either Champion Mine (CM) or Oregon wild type (OWT). The results are obvious (Table 1). The early selection program left needle spot incubation and retarded canker appearance unchanged. But rather dramatic differences between CM and OWT are seen for infection efficiency, needle drop, stunted-infected, mortality period, and infection free second year. Similarly, changes in levels of resistant mechanisms are striking (Table 2) with an almost complete elimination of the fungicidal-short-shoot mechanism.

Table 1. Summary of Pinus monticola family means for 7 resistant control pollinated (RCP) and 13 untested open-pollinated (UOP) families for 7 kinds of responses to inoculation with 2 Oregon wild type (OWT) and 3 Champion Mine (CM) sources of Cronartium ribicola

Symptom	Units	Pine - rust combination			
		RCP-CM	RCP-OWT	UOP-OWT	UOP-CM
Needle spot incubation period	months	4.6	4.5	4.5	4.6
Infection efficiency	spots/spore	.00034	.00018	.00027	.00047
Infected needle drop	$\frac{\text{no. no spots}}{\text{no. in family}}$	.10	.45	.11	.05
Retarded canker appearance	$\frac{\text{no. cankered 2nd yr}}{\text{no. cankered 1st \& 2nd}}$	.06	.07	.06	.04
Stunted infected	$\frac{\text{no. stunted leaders}}{\text{no. canker 2nd yr}}$	.46	.20	.24	.39
Mortality period	months	22.3	23.1	22.6	22.1
Infection free 2nd year	$\frac{\text{no. clean}}{\text{no. family}}$	.08	.48	.04	.01

Table 2. Summary of 7 resistant control pollinated (RCP) and 13 untested open-pollinated (UOP) Pinus monticola family means for occurrence of 3 kinds of resistance mechanisms after inoculation with 2 Oregon wild type (OWT) and 3 Champion Mine (CM) sources of Cronartium ribicola

Symptom Combinations			Proportion in Pine-Rust Combination <sup>1</sup>							
Infected needles After 1 Year	Cankers	Resistance <sub>2</sub> Mechanism	RCP-CM <sup>3</sup>		RCP-OWT		UOP-OWT		UOP-CM	
			N	X/N	N	X/N	N	X/N	N	X/N
Absent	None	PNS	32	0.38	76	0.80	35	0.23	25	0.16
Absent	Appeared 2nd year	RCA	20	0.250	15	0.47	27	0.37	21	0.14
Present	None	FSS	220	0.0004	92	0.24	277	0.01	443	0.002
Present	Appeared 2nd year	RCA	211	0.005	70	0.05	274	0.03	442	0.004

<sup>1</sup>Number of seedlings in each pine-rust combination is: RCP-CM = 252; RCP-OWT = 168; UOP-OWT = 312; UOP-CM = 468.

<sup>2</sup>PNS = premature-needle-shed and is defined as infected needles present at 9 months, absent at 12 months, and no canker at 24 months; RCA = retarded canker appearance; FSS = fungicidal short shoot and is defined as infected needles present at 9 months and 12 months and no canker at 24 months.

<sup>3</sup>X = number of resistant seedlings; N = number in symptom combination.

Here, too, are some possibilities for development of genetic markers to advance the study of C. ribicola genetics. The Champion experience also shows us how fast a resistant population can be eliminated and gives the most substantial evidence to date in support of development of a firm, integrated rust management plan that relies as much on other control options as it does on resistance. It shows, as well, that resistance breeding is going to be a constant vigil. Successful production of white pine will not be a simple matter of producing and then planting one, or a few, generally resistant populations of white pines.

### Conclusions

In summary, a few traits have been recognized and some possible experimental approaches to the genetic study of blister rust identified. The next step is to make rust crosses. Artificial crosses have not been successfully completed for any member of the genus Cronartium. If progress is to be made in understanding rust genetics, we must pass this roadblock. Knowledge about the genetics of C. ribicola is essential to understanding blister rust epidemics sufficiently for construction of an effective and stable rust management system.



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## WHAT CAN BE LEARNED FROM AGRICULTURAL PROGRAMS

R. J. Hoff

The most recent review of plant diseases was published in five volumes from 1977 to 1980. The set is called "Plant Diseases", An Advanced Thesis, Edited by James G. Horsfall and Ellis B. Cowling. If anyone here would like to know more about diseases, including all aspects of disease resistance, you should start with these books. This paper was prepared exclusively from these books.

Man has been aware of diseases ever since he started to cultivate crops thousands of years ago. Followers of the Old Testament thought that diseases were punishment meted out by Jehovah. The Romans had two gods for the rust of their grain, "Robigo" and Robigus." But it wasn't until the development of a microscope in 1667 by Robert Hooke that people began to associate fungi with diseases. And, still it wasn't until nearly this century that things really began to happen. J. C. Arthur became the first professional plant pathologist; now there are 3,000 in the U.S. and 9,000 worldwide. Also, the field of genetics got its start in early 1900. The first Mendelian inheritance of disease resistance was observed in 1905 by Biffen. Stakman in 1917 made Mendelian inheritance pay off in rust control. And then the production of knowledge concerning all aspects of disease, the use of this knowledge in practical problems, and the problems associated with evolving systems snowballed. And so today we really know a lot about

disease. In fact, there is so much known that it still isn't incorporated into our thinking processes.

One thing that I really liked about Horsfall and Cowling's plant disease books was that at the end of Volume 5 they list 454 major principles of plant diseases. To me that was one of the major achievements of these books. Eighteen worked together to develop the list. These principles summarize the present knowledge in plant diseases.

I have chosen 68 of these principles that I think are most relevant to this meeting. Again, I suggest going to the set to get a complete dose of the principles (Vol. 5, pages 519-534). Also, listed with the principles are the page and volume number so that it can be used as a subject index.

Selected Major Principles From Horsfall & Cowling, 1980

1. Disease is the exception not the rule. Most plants are healthy, so in general plant defenses must be sound.
2. Every host-pathogen interaction is unique.
3. Plants vary in susceptibility with age, time of day and time of year.
4. Resistance to pathogens is more common than susceptibility.
5. Introduced pathogens often cause destructive epidemics.
6. Biological fitness is the relative ability to persist over time: it is the most important driving force in evolution.
7. Disease usually spreads more slowly among plants at wide spacings.
8. Plant defenses may be performed or induced.
9. Plants cannot defend themselves by retreating from the pathogen.

10. Escape from disease is a dynamic process. Fast germination of seed and seedlings often result in escape because of a shorter time in a vulnerable state. Fusiform rust on secondary needles must race down a growing needle to get to the stem before tissues harden.

11. Escape from disease is universal among host plants.

Even when there is no specific resistance not all plants become diseased in most years and in most areas. Escape can be managed by using disease-free, vigorous seed, proper planting date and site. Escape can be "bred" into new varieties by producing early or late varieties depending on the disease.

12. Tolerant plants grow well despite insults from pathogens.

Tolerance is the ability of a cell, plant, or field to perform acceptably while providing the habitat necessary for the pathogen.

13. Plants form various physical defenses in response to infection by pathogens including envelopment of pathogens at cell surfaces, deposition of papillae, and general thickening of cell walls.

14. Plants can sacrifice a few cells so that the whole plant can survive.

A plant is highly sensitive to an infecting pathogen often resulting in an early collapse and death of infected cells. This is termed hypersensitivity and is very common in plant diseases.

15. Until recently hypersensitivity was considered one of the most effective and widely distributed mechanisms of resistance in higher plants.

16. Many pathogens induce premature abscission of leaves, fruit, or flowers.

This is amputative type resistance. It is fairly common with crop plants, and we have observed it in the western white pine, white pine blister rust system. Infected needles drop off before the fungus can grow into the stem.

17. Induced resistance requires that energy be expended only when it is needed.
18. Constitutive resistance requires continual synthesis and metabolism.
19. The goal of agriculture is to optimize crop productivity.
20. Integrated management strives for enhancement of natural defenses against disease.

21. Integrated pest management is a philosophy by which ecologically and economically optimum strategies and tactics are developed and applied in crop production.
22. Epidemiology sets the strategy for disease management. That is, populations are managed, not individuals.
23. Absolute control of disease is impossible.
24. Disease control implies finality whereas disease management implies an ongoing process.
25. Education of practitioners must include both the theory and the practical arts of disease management.
26. Plant diseases are not uniformly distributed over the range of their hosts. A resistant culture may have just the right amount of resistance for an area but not enough, or too much, for another.
27. Biological control is the deliberate use of one organism to control another.
28. Hypovirulence and hyperporositis are promising methods for management of certain biotic pathogens.
29. Host resistance is a powerful tool for disease management.

30. The "ideal" way of managing plant diseases is the use of resistant varieties.
31. Control of environment is a powerful tool of disease management.
32. Tolerance is disease without loss.
33. Tolerance is a useful tool of disease management.
34. Disease escape is a useful method of disease management.
35. Rarely does a single factor alone confer resistance.
36. Race-specific resistance has generally been short lived.
37. Genetic and cytoplasmic diversity must be maintained in all major crops.
38. Many agricultural crops are genetically uniform and therefore vulnerable to epidemics.
39. Genetic heterogeneity among host plants promotes escape.
40. Polygenic resistance reduces the rate of disease development.



41. Many plant breeders are "lured" onto the Lorelei rock of monogenic resistance.
42. Plant breeders usually use major gene resistance.
43. Breeding for tolerance may result in long-term pathogen stability.
44. Wild relatives of crops constitute a vast gene pool for diversity.
45. Wild relatives of crop species generally do not possess absolute immunity.
46. Disease can be controlled with chemicals.
47. Resistance to specific chemicals develops quickly; resistance to broad-spectrum chemicals develops slowly, I 336-337.
48. Epidemics result from the conjunctions of host, pathogens, weather, and tissue.
49. Introduced pathogens often induce destructive epidemics.
50. Epidemiological thinking has revolutionized resistance breeding and disease management.

51. Modelling and forecasting of epidemics helps identify gaps in our knowledge of disease processes.
52. Every rational person indulges in forecasting.
53. A forecaster is a prophet and a prophet has his troubles.
54. Biotic pathogens are normal components of all natural ecosystems.
55. Organisms are constantly evolving.
56. Biotic pathogens have co-evolved with their hosts.
57. Co-evolution leads to a dynamic balance between hosts and pathogens.
58. Endemic disease results from a balance between host and pathogen populations.
59. The population that is best adapted to a particular ecological niche will become dominant in that niche.
60. Managed ecosystems usually contain less diversity than natural ecosystems.

61. Epidemics are more virulent on cultivated than on wild hosts.
62. Epidemics rarely result in complete destruction of the host population.
63. Natural ecosystems vary greatly in amount of diversity.
64. Genetic diversity buffers natural ecosystems against disease.
65. Epidemics seldom become pandemic in natural ecosystems.
66. Most pathogens of forest trees are fungi.
67. Uniform forests are susceptible to epidemics.
68. Diverse forests are resistant to epidemics.

One of the most important things to learn from the agriculturist is that a combination of research, developmental, and practical teamwork works best. Researchers find new knowledge, test hypothesis, develop theories, and share in the developmental aspects of management plans with practitioners who are usually the ones who have to make the hard decisions on what to do for each host-pathogen couplet.

Some key points that I think need particular emphasis in respect to forestry are: 1. Diseases are not going to disappear. Thus, we have to learn to manage them. 2. One management tool probably will not work by itself so a combination of some sort must be devised. 3. Single immunity resistant genes will not work by themselves so we must rely on polygenetic resistance, tolerance, or single genes in combinations. 4. We should be diligent to maintain resistance to endemic diseases and use management methods that fit in with the "balanced system".

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VERTICAL RESISTANCE

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In 1963, Vanderplank (15) coined two terms to denote the way plants resist disease. The terms were descriptive of gene action in a strictly dichotomous concept of resistance: vertical resistance (VR), that conferred protection against some races of a pathogen but not others, and horizontal resistance (HR), which was uniformly effective against all races. VR was usually simply inherited and dramatic in effect, but unstable and temporary; HR was usually complexly inherited, gave incomplete protection, that was more difficult to recognize and measure, but was stable and enduring. Although both phenomena had long been recognized under a variety of other names, Vanderplank's work was a watershed, because it crystallized confusing and conflicting perceptions of resistance into a coherent hypothesis. It stimulated much research and probably more controversy than any other conceptual development in resistance breeding. The timing was ripe. It is useful to briefly examine why.

In the early part of this century, following Biffin's discovery that disease resistance could be transmitted like any other Mendelian trait (1), the prospect of nearly complete protection offered by genes with visible, major effects was extremely attractive, and breeders lost no time in searching for them. Concepts of epidemiology and host-parasite interactions were undeveloped, and the task seemed only to require sufficient perseverance. It was not long, though, before breeders found that the protection conferred by resistance (R) genes in some parts of a crop's range was being eroded in other parts, sometimes with greater damage to the improved variety than the original one it replaced. New R genes were sought and used, but the pattern repeated with distressing regularity. Physiologic races of pathogens had been discovered--in many crops, in ever increasing numbers and baffling complexity. In stem rust of wheat alone, they numbered in the hundreds. Understanding of their origin and genetic structure was naive. Races were often conceived as taxonomic units on their own, rather than combinations of genes, in spite of Craigie's work showing that selfing a single race of Puccinia graminis yielded many new races (5).

Light finally was shed by Flor's gene-for-gene hypothesis, derived from his classic studies of the flax-flax rust pathosystem, done in the late forties (6). By careful selection and control of genotypes of both host and parasite, Flor was able to show that for each gene conditioning resistance in the host, there was a corresponding, specific, and complementary gene for virulence in the pathogen. Gene-for-gene relationships were soon found in many other pathosystems of diverse taxa, including both obligate and nonobligate. In the host, these were Vanderplank's genes for VR. Flor's brilliant unravelling of the genetic interactions in his test system did little at the time, however, to alleviate the practical situation at hand. By mid-century, so many VR genes had been rendered ineffective in so many crops by selective increase of virulent mutants in their pathogens that the initial enthusiasm for these spectacular genes turned into widespread discouragement.

Yet, it had long been recognized that low levels of resistance (e.g., slow rusting) in certain varieties of many crops sometimes gave considerable protection, if not freedom, from disease. It is pertinent to note that Flor himself avoided use of test materials of intermediate reaction. He deliberately chose host/isolate combinations of clear-cut phenotypes for his analyses, for understandable reasons: it is much more difficult and less certain to categorize phenotypes of intermediate reaction, especially if they are affected by environmental variance, as they usually are. It was the low level, or intermediate reactions that were controlled, in Vanderplank's view, by genes for HR. HR was usually (though not necessarily) polygenically inherited; effective, if not dramatic; and, by definition, nonrace-specific and therefore stable. It was the last attribute of HR--its axiomatic

stability--that was responsible for much of the ensuing controversy. Vanderplank (16) was adamant, however, and his definitions and discussions admitted no compromise: there were two kinds of resistance; they were controlled by genes fundamentally different in evolutionary origin and mode of action; VR genes interacted specifically with genes for virulence, but HR genes were neutral and did not. The argument polarized thought between those who accepted it at face value and those who saw it as a hypothesis to be tested. It is not difficult to see why. With VR genes in widespread disrepute, HR was seen by many as a panacea, if one were willing to settle for less than complete protection. VR genes could be included in the breeding program, if available, but as incidental supplements. Some (though not Vanderplank) advocated abandonment of VR altogether.

The prejudice against VR continues, and can be heard among our own colleagues in forestry, or seen in the literature. There can be no argument about the weaknesses of VR, as depicted by Vanderplank and many others; the many apparent failures are too well documented. But genes for VR are still used and will continue to be used. In fact, "...genes [for VR] did not fail...they controlled races they were released to control" (3). It was the way they were used that failed--as simple, quick fixes to an acute problem posed by an emergent virulent race. A large part of the problem was that the unit of focus was on the individual plant genotype, rather than the population as a whole. It was presumed that a single resistant genotype, multiplied enough times, would result in an entire crop that was resistant. This view ignored the enormous adaptive capacity and reproductive potential of microorganisms when under severe selection pressure. Wiser strategies have since developed, concisely summarized by Nelson (10).

Multilines. A multiline is a mechanical blend of different genotypes, each of which has a different gene for VR. The background genotype may be uniform, to conform to agronomic standards, but is not a necessary condition. With trees, diverse background genotypes, as with open-pollinated or full-sib families derived from select trees in the wild, or mixtures of different clones, would theoretically work just as well and probably even better, simply because of their diversity. This artificial mixture of genotypes mimics the genetic diversity found in natural ecosystems, where diseases are common, but epidemics rare (2).

VR genes function epidemiologically by sanitizing all incoming inoculum lacking the matching genes for virulence, thereby precluding such inoculum from epidemic involvement. Thus, in a hypothetical case of poplar and leaf rust, a clone among several others with different VR genes would be susceptible only to those spore genotypes in the initial heterogeneous mixture that had the specific complementary gene for virulence. Some disease would inevitably occur, but the race infecting one clone would not attack and build up on adjacent clones because the necessary (different) virulence gene probably would be lacking. Thus, disease would be reduced to endemic levels, a characteristic of HR. The likelihood of "super" races arising with several or all of the matching virulence genes for VR genes in the clonal mixture is a matter of genetic probabilities--the compound function of mutation rates at each locus in question from the avirulent to the virulent condition. The end result is that genes that are individually and genetically classified as VR function collectively and epidemiologically as HR in the population. The efficacy of multilines has been demonstrated experimentally and operationally. For example, different VR genes in as few as 30 to 50 percent of the plants gave adequate and stable protection to oat populations against crown rust and powdery mildew in both natural and agricultural ecosystems (2, 3).



Gene deployment. The idea behind gene deployment is to break up the epidemiological unity of a pathogen by strategically placing different VR genes in different regions of a widely grown crop. A virulent race that built up to epidemic proportions in one region would be severely attenuated upon contact with the next. The action of gene deployment is thus analagous to multilines, but on a geographical scale. It is mechanically easier, and probably cheaper to manage, but has greater risk because of the damage that may be sustained in any given region with the advent of a new race. Where only a few genes have been identified, it may be the only realistic option. Where many genes are available, it can be combined with the multiline strategy. Both strategies should be readily adaptable to forestry.

Gene pyramiding. Nelson (10) advocated the use of several to many VR genes in a single genetic background. To overcome such multifaceted resistance, a pathogen race would have to evolve by simultaneous or stepwise mutations at all the relevant matching loci for virulence. Genetic probabilities are again an issue. For those who do not underestimate the huge reproductive potential of microorganisms, the danger of this approach is in risking all the VR genes in one throw of the dice. But Nelson also argued that VR genes exhibit residual expressions of resistance, even to races having all the necessary genes for virulence. In wheat, certain VR genes "defeated" by isolates with matching virulence genes nevertheless measurably reduced sporulation and infection efficiency of powdery mildew (9, 12), and reduced pustule size and sporulation of stem rust (11). Furthermore, the effect of these genes was greater when interacting in gene pyramids than when acting singly (11, 12). These effects traditionally have been attributed to HR.

Stabilizing selection. Another of Vanderplank's (16) more controversial ideas was that of stabilizing selection. He argued that complex races of pathogens--i.e., those with more virulence genes than needed to overcome existing VR genes in a host--were less fit on these varieties than those with only the right number and combination of virulence genes. Accordingly, complex races would tend to decline in frequency, through natural selection, when simpler host genotypes were encountered. A practical implication was that population shifts of pathogens to higher levels of virulence could be curbed by the way VR genes are managed--in particular through the gene deployment or multiline strategies. The concept is especially attractive for controlling epidemic diseases of forest trees, where plantations of improved genotypes would often be interspersed among wild populations. On the latter, selection pressure on pathogens would be reduced, and the frequency of more virulent genotypes attenuated through genetic homeostasis.

The underlying premise for stabilizing selection was the equation between genetic simplicity (for virulence) and fitness. The evidence for it cited by Vanderplank (16) was largely circumstantial, but impressive. Racial surveys of several pathosystems, including late blight of potato, wheat stem rust, and fusarium wilt of tomato, over wide areas, showed that the simpler races did usually prevail in fields where simple hosts--those with no or few VR genes--were grown. However, there were some notable and consistent exceptions, of which one example will suffice. Race 4 of potato late blight was frequently found where it was "unnecessary," i.e., where there was no matching gene for VR. To explain this and similar inconsistencies, Vanderplank proposed his "strong" and "weak" gene hypothesis. VR genes are weak, like R4 of potato, if races able to match them are equally fit to survive on hosts lacking them; they are strong if the opposite is true. Without further evidence, the argument can be viewed as a convenient means of avoiding the fact that complex races can be fit (10).

The concept and evidence for stabilizing selection were exhaustively evaluated by Nelson (10) a decade ago. There were enough instances of relatively complex races of pathogens predominating on numerous crops where their virulence genes were unnecessary, to invalidate the hypothesis as a universal phenomenon, without invoking the strong and weak gene argument. The critical experimental evidence was also conflicting, and Nelson concluded that fitness and virulence, per se, were not associated.

So much for the history and use of VR, with my acknowledgement that the treatment has been superficial. Of more immediate relevance to the problems we confront in forestry, in my view, is whether the strict separation of resistance into vertical and horizontal components has any basis in reality. Much of the recent literature suggests that it does not. The titles of my assignment and the paper to follow imply that it does, and that acceptance of this dichotomy persists. So, at the risk of trespassing on my colleague's territory, I will spend the rest of this essay challenging that assumption. I do so because I think that accepting it without reservation may have negative consequences for the way we think about resistance. And the way we think about it affects the way we attempt to use it.

The reality of VR is not in question; the evidence for clear-cut, differential interactions among host and parasite genotypes is overwhelming. The crux of the matter is whether HR, as Vanderplank defined it, exists, or is only "...an artifact of experimental procedure," as Ellingboe (5) claims. A problem at the outset is that the most basic attribute of HR--its neutrality and stability to different races--can never be proven because it is impossible to test a host against all possible races of a pathogen. An untested race may be lurking, or arise, that will overcome the apparent HR. Browning et al. (3) give a vivid example of the danger of prematurely attributing HR to a variety. An improved oat cultivar that exhibited rate-reducing resistance (a characteristic of HR) was tested in 11 different single-race rust nurseries. In 10 of these, it showed the same kind of resistance it was developed for; but in the eleventh, it proved highly susceptible. Its resistance was, in fact, race-specific. As the authors commented, the virulent race could as easily have appeared years after the variety had been released and grown extensively.

Ellingboe (4) stated, "There are no data which convincingly show that this latter phenomenon [genetic factors that affect the rate at which an epidemic can develop] is controlled by genetic interactions that are different from the gene-for-gene interactions." The statement is worth examining, because rate-reducing resistance is the way HR functions, according to Vanderplank.

There are several components of rate reducing-resistance (14), including resistances to infection (the proportion of spores forming lesions), colonization (lesion size, pathogen growth rate), and reproduction (amount of spores produced), all of which have traditionally been accepted as being under polygenic control and exhibiting HR. In fact, recognition of any of these components in a crop or tree has often been taken as prima facie evidence for the presence of HR. Herein lies the danger: for once accepted and labeled as HR, the mechanism becomes stable, by definition. Yet experiments designed and executed with sufficient precision increasingly show that not only are the components of rate-reducing resistance race specific, but often under mono- or oligogenic control. Differential interactions were found among varieties and isolates for spore production in yellow rust of wheat (7), and similar results were reported for leaf rust of barley (13). In field tests with rice blast, only modest variety-isolate interactions for rate-reducing resistance were found but much greater interaction for two components (disease efficiency and latent period) were observed when tests were done in growth chambers (17, 18). Other examples can be found in Parlevliet's (14) review.

A critical test of Vanderplank's hypothesis was described by Ellingboe (5) in a two-pronged approach using powdery mildew of wheat. In the first, the inheritance of apparent HR was analyzed in the variety Genesee, long noted in field tests for slow-mildewing. This is a rate-reducing resistance, which, in this case, is associated with a longer latent period. When Genesee was crossed with several fast-mildewing varieties, F2 progenies showed, in greenhouse tests, a range in resistance arrayed in the continuous distribution expected of polygenically inherited HR. But when a second sample of F2's was inoculated and kept in controlled environment chambers, there were only two phenotypic classes, which segregated in a 3 slow:1 fast ratio. Subsequently, a race capable of causing fast mildewing on Genesee was found. Thus, slow mildewing was not only race specific, but controlled by a single dominant gene. Its detection depended on the experimental approach used.

A second set of experiments was designed to determine the effect of an identified gene for VR (Pm4) when it was challenged by different mildew isolates with the necessary complementary gene (p4) for virulence (8). To races lacking this gene, Pm4 confers near immunity (infection type 0). The approach was to see if, under carefully controlled conditions, Pm4 would demonstrate effects typically associated with HR. Results showed that pathogen growth was attenuated and infection efficiencies reduced by up to 80 percent of controls (host isolines with pm4, the recessive alternate allele giving type 4 infection), depending on the isolate used. Similar "residual effects" of other "defeated" Pm genes have been found (9, 12).

I would not disagree with the argument that the examples cited above are too few to dismantle Vanderplank's hypothesis. But when traits with all the attributes of HR, when critically evaluated, are found to be race specific and simply inherited, while VR genes of known major effect also are seen to show properties traditionally ascribed to HR, isn't it time to question whether the hypothesis is still useful?

My objective has not been to argue the relative merits of VR and HR, or to establish that all resistance operates on a gene-for-gene basis, as some claim. These issues are somewhat academic to our problems in forestry, in any event, because so few genes for resistance have been clearly identified. My point is that the merits of resistance genes, or resistance mechanisms of undetermined inheritance, should be evaluated individually, and not forced into categories that carry preconceived notions of their properties, especially stability. Gene function is not altered by a label we attach to it. Clifford's often quoted statement is still appropriate: "In common with other workers, the author accepts the convenience of cataloguing resistance into two types. Nature, I am sure, never intended this division," to which Parlevliet added, "Resistance cannot be classified unambiguously into two groups, nor is there an easy way to discern stable from unstable resistances" (14).

Theory evolves. As scientists, we are enjoined to define, clarify, and explain causal mechanisms. As practitioners, it is enough to use what works. It is important that our concepts serve our practice, not vice versa.

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## HORIZONTAL RESISTANCE

R. J. Hoff

There are two major kinds of resistances: those that inhibit infections and those that inhibit growth of the pathogens after infection. The first is commonly called vertical resistance, specific resistance, major gene resistance, and others. The second type has been called horizontal resistance, non-specific resistance, minor gene resistance, general resistance, field resistance, polygenic resistance, partial resistance, uniform resistance, durable resistance, dilatory resistance, slow rusting, and slow mildewing.

All of these terms are useful for a particular circumstance. But none of them are acceptable in a general sense. At the present time, horizontal is probably being used by a majority of breeders.

Basically all of these terms describe one thing--a slowing down of the growth and multiplication of the pathogen after infection, i.e., a rate-reducing resistance.

Whereas vertical resistance is controlled by single genes that impart immunity, but not always so; or susceptibility depending upon the presence of a specific pathogen race, horizontal resistance is usually controlled by polygenes but not always so, and is not generally pathogen specific.

Resistance in natural systems is usually due to a combination of vertical and horizontal resistance. Diversity is a key element for stability. Somehow natural systems have developed a balance between host and pathogen over years of time and yet the balance is dynamic, changing from year to year. Then when we come along and pluck out certain "cultures" that fit our need for grain, fruit, or fiber, the balance is changed. Luckily most pests, endemic or exotic, will remain unimportant, but there will be a few that are going to cause problems. We can't often predict which ones are going to be the problem ones.

For the first 60 years after genetics was established as a science, and host resistance was seen as a genetic trait, the crop breeders emphasized the single, major immunity imparting genes. And why not? Don't we all want immunity. A survey of 900 papers from 1912 to 1970 showed that 840 dealt with the single gene type resistance, leaving only 60 on horizontal resistance; and most of those were before 1950. The crop breeders found that the vertical resistance was generally ephemeral. But most damaging was that they found that after breeding for single gene for several generations, a variety ended up more susceptible after new races had developed. Although this has been observed for many years, only recently has there been an answer for this effect. What was happening was that the horizontal resistance genes were being lost (something that van der Plank called the vertifolia effect).

The prevailing view in crop breeding today is to emphasize horizontal resistance. Vertical resistance is still useful in many instances and with particular diseases. It seems that a combination of both is ideal.

In forestry, the price for mistakes is very high, at least in terms of years lost. A loss of a single gene variety prior to commercial thinning would mean we would get nothing, and it would take many years to produce a new variety. Thus, it is imperative that the breeding portion of insect and disease control emphasize horizontal resistance.

In natural systems we have to be on the lookout for those insects and diseases that will become pests and thus be able to adjust the breeding programs to include resistance, especially horizontal resistance.

With introduced pests, we will just have to hope that there will be sufficient variability in the species to be able to develop a resistance level that is economic.

My main concern is with the native pests. I don't think there is any excuse now of so badly screwing up the balance that a native pest would become epidemic. We all need to make sure that field tests or artificial inoculation tests are run on various host-pest systems in order to monitor the change in the line of resistance.



## SELECTION METHODS

It is easier for me to discuss selection methods by using the western white pine blister rust as an example.

Horizontal resistance mechanism.

1. Reduced needle lesion frequency. Although this trait seems to effect the initial inoculum and not growth rate, it does behave like an HR type in the sense that it is quantitative and that nearly all individuals are infected.

2. Appearance of stem systems. The data used is the ratio of stem symptoms 1 to 4 years after inoculation.

3. Slow canker growth. The data used here is from the older progeny test, i.e., 1952, -53, -54, -55, -64, -65, and -69 progeny tests. About 2 percent of the original trees have living cankers that are growing slow enough so that the trees have not become girdled.

4. Bark reaction. Some bark reactions are definitely an immune-type reaction typical of vertical resistance. However, there are others that cause cankers to advance differentially over the years. Microsections of cankers from the slow canker growth thus look similar to microsections of bark reactions. The main difference may be the presence of a wound-periderm in bark reaction that so far appears to be missing in the slow canker growth trees. One type would be the very quick, small bark reaction right at the fascicle base. The other type is one in which the fungus is "killed back: from time to time. Anatomically, the reaction appears the same as the first bark reaction; the fungus just seems not to be completely killed out.

For this paper I will consider the first three as horizontal resistance. Even with these, we do not know much about their mode of action or their genetics. Anyway, here is a suggestion:

Four years after inoculation of 2-year-old seedlings, select families with:

1. low needle lesion frequency,
2. slow stem symptom appearance.

Select individuals within these families with:

1. no spots, no stem symptoms, and low number of spots,

2. premature needle shed, no stem symptoms, and low number of spots,
3. fungicidal short shoot, no stem symptoms, and low number of needle spots,
4. Bark reactions and low number of needle spots.

Establish a seed orchard in four adjacent sections:

No spot	Premature needle shed	Slow canker growth trees grafted into seed orchards
Fungicidal short shoot	Bark reactions	

and intersperse within this seedling seed orchard grafts of trees that were inoculated in the earlier progeny tests that have old basal cankers that have grown less than one-half the bole circumference. Frequency of these grafts in the seed orchard--20 percent.

Estimated resistance:

vertical resistance - about 60 percent

horizontal resistance - increase by 25 percent?

The level of vertical resistance can be adjusted by the size of sections. A large size would increase the level of resistance because there would be less interchange of pollen among all sections.

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# PROGENY TESTING THE SOUTHERN PINES

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## Abstract

Artificial inoculation procedures and field designs for progeny testing have been established for fusiform rust resistance in loblolly and slash pine and brown-spot resistance in longleaf pine. Research results indicate that extensive testing is needed if gains are to be made in developing resistant strains.

Keywords: Fusiform rust, brown-spot, needle blight, Pinus elliottii, Pinus taeda, Pinus palustris

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Progeny testing is a necessary component of every southern pine tree improvement program. Designs and objectives may vary, but no program operates without a progeny testing component. All progeny tests invariably include various combinations of three objectives: (1) to determine the genetic worth of parents (often for seed orchard roguing purposes); (2) to provide advanced generation material for further selection; and (3) to compare improved against a woodsrn, orchardrun or other control material. When these objectives are coupled with simultaneous selection for a myriad of traits, the need for correlating juvenile and mature traits, the inclusion of material from several breeding designs and levels of improvement, and the requirement that genotype by environment interaction be examined, it becomes evident that progeny testing is a complex component of any tree improvement program. Because of all this diversity, there is no single system for design and analysis that is best for every testing situation. However, some useful conclusions can be synthesized from the vast experience of progeny testing across the South. This paper deals primarily with progeny testing for fusiform rust caused by Cronartium quercuum [Berk.] Miyabe ex Shirai f. sp. fusiforme resistance in slash (Pinus elliotii Engelm. var. elliotii) and loblolly (P. taeda L.) pine and for brown-spot needle blight (caused by Scirrhia acicola (Dearn.) Siggers) in longleaf pine (P. palustris Mill.). Both greenhouse and field testing aspects will be covered. The information presented will include research accomplished at the Southern Forest Experiment Station, but with heavy reliance on what is being done in the three southern tree improvement cooperatives--University of Florida, North Carolina State, and Western Gulf. Each of these cooperatives has many industrial and other agency members (Table 1) and, together with the R-8 program, have been the major thrusts of cooperative tree improvement programs in the South (Goddard 1981, Lowe and van Buijtenen 1981, Wier 1981).

Table 1.--Statistics on tree improvement activities for three cooperatives in the South

Cooperative	Date organized	Members	Primary species	Regen- eration	Selected trees	Progeny test	Seed orchard	Maximum yearly production of seed to date
		number		acres/yr	number	acres	acres	lbs
Florida	1954	14	Slash pine Loblolly pine Longleaf pine Sand pine	200,000	2500	----	----	40,000 (1979)
North Carolina	1956	27	Loblolly pine	470,000	3500	4225	3705	56,000 (1980)
Western Gulf	1969	22	Loblolly pine Slash pine Longleaf pine	500,000 <sup>1/</sup>	3300	----	2130	16,000 (1980)

<sup>1/</sup> Planned planting acreage when orchards are in full production.



### Fusiform Rust Testing

Artificial inoculations.--In the late 1950s, progeny testing for rust resistance was done at the Southern Station using moist chambers in the nursery (Jewell and Mallett 1967, Dinus 1972). In these chambers, pine seedlings 21 to 30 days old were exposed to rust inoculum from telia-bearing leaves on small oak branches. Although the system gave consistent results from year to year and family to family, infection rates were high and more flexibility and control of variation was needed for testing and experimental purposes. Subsequently, Snow and Kais (1972) and Dwinell (1972) modified artificial inoculation systems that provided better control of inoculum concentration. At the Southeastern Station in Athens, Georgia, further modifications were made to meet the needs for mass-screening, and a concentrated basidiospore spray (CBS) system was developed (Matthews and Rowan 1972). The CBS system is currently being used at the Resistance Screening Center at Asheville, North Carolina. At the Center, the basic objective of the early progeny testing is to define pine families that are especially susceptible to fusiform rust. These families can then be dropped from programs thereby saving expensive field testing operations. The key to a successful artificial inoculation program is getting good correlation between the greenhouse and the baseline field results for resistance. Recent results using multiple traits to characterize resistance of inoculated seedlings have helped to improve prediction of field resistance. Whereas incidence of swellings explained only 19 percent of the field performance, 62 percent of the field variation was explained by using a combination of the proportion of smooth galls, incidence of disease without swelling, and proportion of fat galls (Walkinshaw et al. 1980).

Field testing.--Although artificial inoculation procedures can serve as a coarse screen to purge the least resistant families and/or select the most resistant families, field testing of all families is routinely practiced. This practice serves to correlate the artificial inoculation system results with field results and to evaluate all families (including the susceptible ones) for growth and form traits. If field testing for rust resistance is to be effective, it is critical that the trees be planted in high rust hazard areas. Even though the rust fungus is present in an area, infection of the trees is not an automatic consequence. Infection is dependent on many factors other than the presence of spores and trees. Testing at several locations improves the chances of a good infection and offers the added advantage of exposing the trees to an array of fungal types.

For slash pine, the best progeny testing guide available comes from the testing experiences of the Florida Coop (Goddard 1981). Progeny testing was initiated in the 1960s using primarily wind-pollinated seed from several ramets per clone in the orchard. Standard tests consisted of 20 to 40 families in 10-tree row plots with 10 blocks per test. Each family was included in at least three tests on at least two site types and in 2 different years. As these tests developed, three important facts became obvious: (1) in general, orchard progenies showed little or no superiority over checks for fusiform rust resistance; (2) many tests were in low rust incidence areas and were therefore not effective for screening for resistance; and (3) in tests where rust was present, there was substantial variation in resistance.

This early testing experience led to the development of a large scale fusiform rust testing program. First, open-pollinated progenies of all orchard clones were tested using the oak leaf suspension artificial inoculation technique. Then all progenies were tested in the field at four carefully selected high rust risk locations across the Gulf South. About 1,000 families were screened over a 5 year period.

Starting in 1975, the 45 most resistant families were tested again in nine widely scattered high risk locations (Goddard and Schmidt 1979). Data collection in these tests include: (1) survival at age 1, (2) rust incidence at age 3 and 5, and (3) height and diameter at age 5 or 6. Results from this test show large significant differences among locations and families as well as significant location by family effects. There are several important points from this work. First, although these 45 families were previously screened for resistance, 10 of them were as frequently infected as the control lots. It appears that extensive testing will be required to define resistant families in slash pine. The second point is that single tests or even a series of many tests in low rust hazard areas will not provide much assurance that the truly resistant families are identified. Third, although in this 45-family test the family by location interaction was statistically significant, from a practical standpoint it was not a serious problem. Of the 25 families showing high levels of resistance, 15 were consistently resistant at all nine locations. The tests also suggest that matching specific families to narrowly defined geographic locations will not be practical. There was as much difference in relative ranking of families in tests in close geographic proximity as there was among rankings in tests more widely separated.

Although there has been extensive progeny testing for rust resistance in slash pine, the expected gains from extant orchards is small. Less than 10 percent of the clones provide good resistance, and because of seed production needs it is not feasible to rogue the orchards of all clones with low resistance. Long-term selection and breeding strategy is underway to change the situation. Mass selection under epidemic rust conditions coupled with breeding and progeny testing points the way to a brighter future. Several agencies and companies in the Gulf South have established slash pine seedling seed orchards and are thinning primarily on the basis of rust resistance (Goddard et al. 1982, Powers et al. 1976). Progeny from seed in one such orchard were generally twice as resistant as seed from clonal orchards with limited roguing.

The situation with loblolly pine is quite similar to that with slash pine. In 1977 there were 34 clones whose resistance was listed as excellent and 56 more as good (21st N.C. Ann Rep. 1977). A clone makes the list only after it is rated in various tests for several years. As with slash pine, the test averages vary greatly from site to site and year to year. In the first generation progeny testing program the standard design in the North Carolina Cooperative was for each family to be in two locations in each of 3 years. Six blocks were planted in one location and three blocks in the other, using 10-tree row plots (25th N.C. Ann. Rep. 1981). Measurements were taken on a variety of traits and years. After analyzing the first generation tests, the progeny test design for second generation material was changed. Current procedures for a loblolly test is to plant 30 to 45 families in two environments in each of 2 years, using six trees per plot and six blocks. Trees in progeny tests are measured at ages 4, 8, and 12. These procedures were developed primarily from data on growth traits and should be adequate for fusiform rust evaluations, provided the tests are in moderate or high rust hazard areas.

In progeny testing for fusiform resistant trees, there have been some problems in getting consistent responses under artificial inoculation and field conditions. The pollen mix in the orchard (Powers and Zobel 1978), the geographic location of the test (Goddard and Schmidt 1979) and the fungal isolate used for testing (Snow et al. 1975) have all been identified as being responsible for the inconsistencies. A recent series of six experiments at the Southern Station examined the interaction phenomenon using 22 open-pollinated families and six full-sib families of slash pine and nine fungal isolates of fusiform rust (Bey and Walkinshaw 1981). The pine families were all selected for high field resistance, whereas the fungal isolates that were selected varied from weak to strong in their ability to infect slash pine. Although, a priori, the pine families were judged uniform for field resistance, when inoculated with the nine isolates the average infection by pine family ranged from 27 to 84 percent. Even though the isolates had been judged diverse in their ability to infect the 22 pine families, the average isolate infection ranged only from 47 to 68 percent. The high variation among the pine families and low variation among the fungal isolates suggests that the pine is more variable than the fungus--a fortunate situation from the tree improvement perspective.

Besides differences in average infection, the families also differed in their individual ability to rank the nine isolates. Only 5 pine families individually ranked the isolates similar to the isolates overall ranking; that is, the isolate ranking by these 5 families had a significant positive rank correlation with the overall isolate ranking. In contrast, the individual isolates all ranked the pine families similar to the family overall ranking ( $r = 0.43$  to  $0.79$ ). This suggests: (1) that a relatively few isolates will rank fusiform rust resistance of pine families as well as when many isolates are used; and (2) that a single pine family might rank fungal isolates far differently than the overall ranking when many families are used.

It should be pointed out that there may be room for improvement of the present testing system. One possibility is to test each entry or pine family using many separate fungal isolates. Although it seems likely that the variability in the reaction to the isolates would correspond to the stability of infection in the field, additional research is needed in this area.

Early evaluation of fusiform rust in slash and loblolly pine plantations is based on the premise that the major effect of rust is on reduced yield caused by rust-associated mortality (RAM). Predicting RAM from early infection levels has been the subject of considerable research. There is additional concern that infections can predispose trees to deformities and breakage that decrease quality, but relatively little quantitative information is available. From a yield standpoint, Powers et al. (1974) evaluated three slash pine stands with heavy rust infection and concluded that rust had a definite financial impact, but that losses were dependent on the initial stand density. In a genetic test, Sluder (1977) found significant negative correlations between incidence at 3 or 5 years and survival or volume per acre at 15 years. In another genetic test with loblolly and slash pine, Wells and Dinus (1978) developed equations for predicting RAM on the basis of 3 and 5 year stem infections. The latter two genetic examples of early-mature correlations show that early field screening for fusiform rust resistance will be useful--as a baseline for judging the artificial inoculation technique and for estimating future yield. Recent research by Nance et al. (1981) shows how early incidence of fusiform rust can be incorporated into a slash pine growth and yield model. This makes it possible to quantify genetic losses (or gains) for resistance in terms of yield (volume/acre). This relationship has not yet been worked out for loblolly, but data sets are available and will be the subject of future research.

In summary, it appears that many of the procedures for progeny testing of fusiform rust resistance are established. There is a risk in testing that is associated with uncertain probabilities of infection and some family by location interactions. Because of this, and the fact that only a few percent of the selected families are highly resistant, large and extensive progeny testing programs are needed. More recent progeny tests of trees selected in highly infected stands and seedling seed orchards suggests that greater gains are possible than shown by the results from the initial seed orchard selections. As plans for future generations are made it will become increasingly important that the potential genetic gains be translated into accurate yield estimates through incorporation in growth and yield models. With information on expected gains in volume per acre at rotation age, rational decisions can be made for future progeny testing programs.

#### Brown-spot Needle Blight in Longleaf Pine

Research on selection and breeding for brown-spot needle blight resistance in longleaf pine has been carried on by the Southern Station for more than 20 years (Derr 1963). It had its origin with early researchers like Art Verrall and Paul Siggers who reported observing healthy individual seedlings among heavily infected neighbors (Siggers 1930, Verrall 1934, Derr and Melder 1970). Curiosity about whether certain parent trees were responsible for the resistant individuals led to the first progeny testing. Over the past 20 years more than 1,000 pine families have been evaluated by the Southern Station. About one-third of these families were in tests designed for ranking parents in the R-8 longleaf tree improvement program and two-thirds were in tests designed for answering selection and breeding strategy questions.



To make genetic gain, perhaps no other southern pine is as demanding in the requirement of progeny testing as is longleaf. Traits that are important in early years, like disease resistance, survival, and early height growth, are not detectable in mature trees. Furthermore, form is generally very good in all longleaf, and progenies of generally good quality performed as well as those from rigorously selected plus-trees (Goddard et al. 1973). In view of these findings some tree improvement programs modified their approach from the traditional plus-tree/clonal orchard system (Rockwood and Kok 1977). Emphasis was shifted from phenotypic selection alone to less stringent selection and short-term progeny testing. Large numbers of well-formed dominant trees are selected and only those whose progenies perform well are eligible for use in a grafted orchard. In the Florida Cooperative the progeny tests themselves will be rogued for conversion to low-cost seedling seed orchards. After a series of between family and within family roguings these selections will be available for seed orchard establishment (Goddard 1981).

Within the framework described above, brown-spot in longleaf pine has been evaluated in numerous tests at the Southern Station. In all the field tests, if brown-spot inocula were present there were large differences in infection levels among families. In one open-pollinated test of 227 plus-trees, resistant seedlings per family ranged from 2 to 89 percent (Derr 1971). Even with large family differences in brown-spot infection, selection is not a clear cut procedure. In a test of 60 families at the same location in separate years, the correlation for family means for heights was only 0.31. The lack of correlation is not too surprising, for the brown spot infection was more severe in the first test than the second (55 versus 40 percent). This suggests that progeny tests need to be replicated over several locations.

Another study of 540 parent trees showed a significant family by location interaction and suggests that progeny testing needs to be done in the area where the seed is to be used. For 3-year height data, the top 5 percent of the trees selected for Mississippi were, on the average, in the 42nd percentile in Louisiana. Only 1.5 percent of the families appeared to be adapted to both locations (Snyder and Bey 1978).

Similar to the poor correspondence between locations, there is also poor correspondence between family height growth in diseased and disease-free tests (Snyder and Derr 1972). In a 540-family test, three times as many families as expected from the eastern region were in the upper 5 percentile for 8-year growth in plots where brown spot was controlled. In contrast, in the adjacent infected plots, none of the eastern sources were in the upper 5 percentile. In all longleaf progeny testing, especially in the west where brown-spot is commonly present, it becomes essential that progeny testing be done on sites where the disease is present.

A procedure found to work well for field screening brown-spot resistance is to plant test seedlings in a field that contains many natural or planted longleaf seedlings infected with brown-spot. If a test site has no natural longleaf, seedlings can be planted a year or two ahead of the test trees. If the trees are planted about 1 m apart in the row, and if there is a source of inoculum in the area, the disease will build up on the source trees in a couple of years and serve as prime infection-spreaders for the test. The test trees can be planted in between, and one can be assured of a good test for resistance. Prior to establishing a test in an area with natural longleaf, it works best to scalp a narrow strip for the test row. The bare soil encourages rain splash and the spread of conidiospores of the fungus which infect the test trees. Field testing designs have varied from single to 20-tree row plots, with 4 to 20 replications, depending on the study objectives. For the purpose of ranking families in the absence of brown-spot, the Florida Coop uses 12 replications of 5-tree row plots.

Brown-spot evaluations are done on a seedling-by-seedling basis with a quick ocular percent estimate of the amount of needle tissue that is necrotic. Estimates are always done in the fall when the maximum amount of foliage has been exposed to the fungus. Brown-spot evaluations in the field should be done after there is a good build-up of the fungus, but while the trees are still in the grass stage. This will vary depending on amount of natural inoculum present, the site quality, the seed source, size of seedlings planted, and the weather. Usually good differentiation for brown-spot resistance will occur 2 or 3 years after field planting, about the time of height growth initiation.

Greenhouse testing using artificial inoculation offers promise for screening for brown-spot resistance (Kais 1975, Kais and Bey [in press]). The basic procedure involves growing seedlings and evaluating for brown-spot in a 6 to 8 month period. Seedlings 3 to 4 months old, growing in super cells, are enclosed in moist plastic bags for 3 days, inoculated with a 100,000 spore/ml suspension, and then rebagged for 10 days. Plants are grown in the greenhouse under 14 hour days until brown-spot readings are taken 3 to 4 months later. The readings involve ocular percent estimates of the amount of needle tissue that is necrotic. A recent test compared the correlation between greenhouse and field evaluations. On a family basis there was generally good correspondence between greenhouse brown-spot ratings and field brown-spot ratings (average for years 1 through 5,  $r = .65$ ) and between greenhouse brown-spot ratings and 5-year survival ( $r = -.69$ ), 5-year diameter ( $r = -.61$ ), 5 year height ( $r = -.53$ ), and early height initiation ( $r = -.69$ ). It appears that greenhouse screening for brown-spot resistance would be useful in programs where field infections are not likely and for the initial purging in screening out the most susceptible families.

In summary, procedures for progeny testing for brown-spot needle blight resistance in longleaf pine in the field and the greenhouse have been partially established. The success in breeding for resistance will depend heavily on screening large numbers of families and the presence of sources of inoculum to obtain infection from the field. Effective screening under greenhouse conditions and early evaluation in field tests points to encouraging prospects for improvement of longleaf pine resistance to brown-spot needle blight.

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RESULTS OF 5 YEAR PROGENY TESTING PROGRAM  
OF Pinus lambertiana & P. monticola  
FOR RESISTANCE TO C. ribicola

PACIFIC NORTHWEST REGION  
U.S. FOREST SERVICE

by  
SAFIYA A. SAMMAN

JULY, 1982

RESULTS OF 5 YEAR PROGENY TESTING PROGRAM  
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INTRODUCTION

Since early sixties, a developmental program for the production of blister rust resistant western white and sugar pine has been conducted by the Dorena Tree Improvement Center in the Pacific Northwestern Region (R-6). The program involved nursery testing with no field plantations. The nursery testing was designed to determine levels of resistance in western white and sugar pine to the blister rust fungus, Cronartium ribicola J.C. Fisch.

This paper will present the results of some of the nursery tests and a description of the plan for field testing of white pines.

MATERIALS AND METHODS

Seed Handlings

Seed from phenotypically resistant trees that are selected from natural stands is extracted, sorted, stored and prepared for planting at the Dorena Tree Improvement Center. Seed is handled in single tree lots. The number of selected tree goal from the tests is 4000 parents for the western white pine and 2294 parents of sugar pine from only National Forest lands. In addition to this goal we have cooperative agreements with other agencies to test and screen their selections.

Standard Crosses

Seed is continuously stockpiled for each of a series of standard crosses. These crosses are used to evaluate and tie together each inoculation within a season and from year to year. The same ten standard crosses are included annually in the screenings to monitor any changes in the rust population. Three more standard crosses are included in every inoculation to standardize the different runs within the same season. These crosses are thoroughly inspected at 9 months for needle infections and 1, 2, 3 and 4 years after inoculation for development of cankers.

Nursery Design

Experience and data at Dorena indicate that 960 families is about the maximum number that can be managed annually. The limiting factor has been number of seed lots available per year, this has ranged from 360 to 1000 seed lots. Inoculation chamber is another limiting factor, it only holds 7200 seedlings at 4x4 inch spacing. A major limiting factor is inoculum availability which has permitted the screening of 8 successive tests annually.

Progeny of 240 families are distributed in the test as follows: 10 seedlings per row plot per replication, 3 replications per test, and 2 successive tests. The basic experimental unit is 20 pallets, each is 40x48 inches arranged in subunits of four for operational purposes. Tree plots are assigned randomly to planting positions. The 240 families are selected to include selections from all breeding

zones within the region. Selections are chosen to sample as many locations of a breeding zone as possible.

The duplication of families, in two runs allows the measurement of variation due to inoculum and environmental conditions during the inoculation. Selection of families from breeding zones permits comparison of infection levels of the different sources.

### Inoculation

Inoculation procedures developed by research were adapted for conditions of the Center in Region 6. Adjustments to the chamber are made as deemed necessary. Inoculum density has been adjusted from the recommended 2000 to 3500 spores per  $\text{cm}^2$  for the sugar pine and 3000 spores/ $\text{cm}^2$  for western white pine. The inoculation chamber measures 45x33x10 feet equipped with a misting and cooling systems.

When the pines are inoculated, pallets are moved into the inoculation chamber. Infected ribes leaves from Ribes garden at the Center and leaves from a minimum of different geographic sites. Ribes leaves are placed on screens 2 feet above the seedlings, with telia-bearing surface facing the seedlings. The leaves are covered with a polyethylene tent to eliminate run-off water from the leaves and monitoring slides.

The inoculum density is monitored with rubber cement coated slides. Slides are removed at 1 to  $\frac{1}{2}$  hour intervals after the first 6 hours until an average of 3000 spores/ $\text{cm}^2$  is reached. The level of inoculum density is assessed by obtaining the average of spore density at five positions per pallet. At appointed time the slides are removed from each of the positions, dried by a slide warming table, stained with a glycerine-aniline blue mixture and covered with a cover slip; then 8 randomly selected fields are counted.

Relative humidity is maintained for at least 12 more hours after removal of leaves. Seedlings are inoculated after 2 growing seasons. Inspection for rust infection is carried on 9 months for needle spots and 3 and 4 years after inoculation for development of cankers.

Detailed analysis of the data collected from all inspections allows selection of best families and best individuals within those families. The inspections maximize selection for several mechanisms of resistance, including both vertical and horizontal resistance factors.

### Results and Discussion

Comparison of the needle lesion data for both western white pine and sugar pine indicated that sugar pine has on the average fewer spots per meter of needles than western white pine. In open pollinated western white pine families number of spots ranged from 1.52 to 7.56 spots per meter of needles with an average of 4.17; while sugar pine families had 1.52 to 3.8 spots per meter of needles with an average of 2.86. The inoculum density for the western white pine and sugar pine ranged 2400-2700 spores per  $\text{cm}^2$ .

Analysis of variance of needle lesion data of western white pine indicated significant differences exist between families (Table 1.). While

Table 1. Analysis of variance of blister rust needle spot frequency in western white pine and sugar pine.

Source of variation	Western White Pine		Sugar Pine	
	df	Mean squares	df	Mean squares
Row	2	7.01*	2	0.65
Column	4	0.86	4	0.08
Error 1	6	1.069	6	0.68
Groups	2	7.92	2	0.0015
Families within groups	117	0.19**	117	0.111 <sup>n.s.</sup>
Error 2	467	0.11	467	0.113

\* Significant at the 5 percent level of probability

\*\* Significant at the 1 percent level of probability

n.s. Non-significant

similar analysis of sugar pine data show a remarkable degree of family sameness for this one trait.

On the other hand analysis of five year mortality data of 3 consecutive years of testing indicated a different story. Both sugar pine and western white pine demonstrated family variation. Thirty two percent of all sugar pine families tested during the period of 1974-76 had survivors with survival of 35% of these families ranging from 5-61%. Full-sib families average survival was 12% while survival of open pollinated families averaged 4%.

During the same testing period 1974-76, 28% of all western white pine families tested had surviving progeny with only 17% of these families having survival above 5%. The overall survival rate ranged from 1-24%. Full-sib western white pine families averaged survival rate 4% while that of open pollinated families 2%.

We can conclude from the results that seed from seed orchard, which contains families with resistance material could be expected to have 3 times the number of surviving individuals as seed collected from selected trees in natural stands or untested material. Families selected to be used in seed orchards have a minimum of 5% survival and a combination of two or more resistant mechanisms. Thus far a total of 9 seed orchards have been established in Region 6. They include material with different combinations of resistant factors.

The results also indicated that a closer investigation of the sugar pine blister rust system should be conducted to evaluate inoculum density resistance mechanisms of sugar pine. A study has been started to evaluate the infection efficiency and classify resistance mechanisms in sugar pine and contrast these mechanisms in western white pine.

The second phase of the testing program is the field evaluation plantations. To date 66 plantations have included western white pine. Seed used for these plantations is from the tested parents in natural stands and the seed orchard at the Center.

In only three of these plantations the identity of the family is kept. The rest are part of general reforestation program in the region. However these three plantations are 15-18 years old; but the only useful data is an estimate of not hazard in the area and no ranking of families is possible. We are in the process of accumulating seed for field evaluation plantations and expect to establish 6 such plantations within 2 years. The objective of the evaluation plantations will be to

1. evaluate resistance of families
2. growth characteristics
3. identify which generation is needed per hazard class.

Each plantation contains material from:

1. Seed orchard and control crosses F1
2. Control crosses from first generation F2
3. Open pollinated seed from test parents
4. Open pollinated phenotypically selected resistant parent
5. Control from a general reforestation seed lot.

Plantation sites are selected to couple different hazard areas within a breeding zone.

We have not yet made final decision on best field design of the plantations, but it has to be one that could meet our objectives.

Seedling Seed Orchards for The Production of Fusiform Rust  
Resistant Slash and Loblolly Pine

by

H.R. Powers, Jr.<sup>1/</sup> and J.F. Kraus<sup>2/</sup>

ABSTRACT

Selections of loblolly and slash pines have been planted in a seed orchard for the production of fusiform-rust-resistant seedlings. Half of the orchard consists of grafted trees of superior clones, while the balance is designed as a seedling seed orchard made up of survivors of artificial inoculation tests. Eventually annual production should exceed 15 million seedlings for planting in areas of high rust hazard.

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The need for seedlings that are resistant to fusiform rust for reforestation programs in the Southern United States has become increasingly obvious over the last two decades. Fusiform rust, caused by Cronartium quercuum f. sp. fusiforme, is the most serious disease of southern pines and a major factor in management decisions across large areas of the South (7). In 1967 the U.S. Forest Service and the Georgia Forestry Commission initiated a cooperative program for the development of rust resistant southern pines. Before this time, many phenotypically superior pines had been selected and put into first-generation seed orchards. Trees were selected primarily for their growth and yield. Rust resistance was a secondary factor, and many selected trees were in old stands that developed when rust incidence was low. Therefore, selected trees may not have been exposed to strong,

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natural selection pressure for rust resistance. Also, branch infections had been lost due to self-pruning and were no longer visible when the selections were made. As a result, many selections did not have high levels of disease resistance.

From progeny tests, however, information was available not only on disease resistance, but also on growth and yield of the progenies produced by crossing the first-generation selections. Initial evaluations were made to select the best families for all characteristics and, within this group, individual trees from families with outstanding rust resistance were selected. Grafts were made from these selections and placed in clone banks for evaluation of rust resistance. The best of these trees were eventually to provide the material for the formation of rust-resistant seed orchards.

Almost all of the rust-resistant orchards in the Southern U.S. have been developed by grafting scions from selected, apparently rust-resistant trees. Unfortunately, the number of clones with proven rust-resistance is relatively low, particularly for loblolly pine. In 1976 I estimated that there were approximately 50 highly rust-resistant slash pine selections available in the entire South, but less than 30 loblolly pine selections of this caliber (Powers, unpublished data). Other selections classified as intermediate in resistance to rust could be added to these numbers. However, this is a very limited genetic base from which to produce seedlings to be distributed over the large area where rust is a critical problem.

Research on rust resistance was accelerated in the early 1970's by the development of a large-scale, carefully controlled artificial inoculation system for evaluating resistance to the disease (4). This inoculation procedure, called the Concentrated Basidiospore Spray (CBS) System, screens large numbers of seedlings by uniformly inoculating them with a specific density of basidiospores. Field progeny tests are still basic to resistance evaluation, but the artificial testing provides results in a fraction of the time required for field tests. CBS results are



correlated closely with those of field tests, and the system selects the most resistant families quite efficiently (5). The survivors from these tests, in particular from the more resistant families, are obviously valuable for breeding programs (1, 2).

The seedling seed orchard approach offers a unique opportunity to combine techniques from both genetics and pathology to maximum advantage. The genetic base of resistant southern pines and the levels of resistance in the selected material can both be increased by utilizing the healthy survivors of artificial inoculation tests in a seedling seed orchard. The production from this type of orchard can eventually be compared with that from a standard clonal orchard.

This paper outlines a procedure for utilizing the rust-free survivors from inoculation tests in an orchard designed for the large-scale production of rust resistant seeds and presents family-by-family data from both slash and loblolly seedling seed orchard blocks at age 5.

#### MATERIALS AND METHODS

As soon as the selections in the clone banks began producing cones, the resulting seedlings were tested with the CBS system. By 1974 it was obvious that many of these selections were producing seedlings far superior in rust resistance to commercially available seedlings. Therefore, in cooperation with the Georgia Forestry Commission, we decided to establish a 24.3 ha (60 acre) production orchard of disease-resistant material equally divided between slash and loblolly pine. Because of the relatively low number of resistant selections available, one-half of the acreage for each species was designed as a standard clonal orchard, and the other half as a seedling seed orchard. One aspect that was completely new was the use of survivors of the CBS tests to form the seedling seed orchard.

The clonal orchard was planted at standard 9.1 x 9.1 m (30- x 30-foot) spacing, with each 0.4 ha (1 acre) block containing 49 grafts. Most trees were grafts of second-generation selections, but a few of the best first-generation selections

were included to produce 49 different clones per block.

Seedling seed orchard blocks contain 50 replications. Each replication includes a randomly placed single tree of each family included in the block. All seedlings used in these plantings were survivors of artificial inoculation tests and were gall-free 9 months after inoculation. Usually seedlings of 12 to 16 families were included in each block, and a total of 93 and 76 families are represented in the loblolly and slash orchards, respectively. These families were rated as resistant following inoculation tests and in some cases, also on the basis of field progeny test data. Seedling seed orchard trees are spaced closely; in our case, 1.5 x 4.6 m (5 x 15 ft). As selection proceeds it is necessary to thin heavily in order to reach an eventual spacing of approximately 9.1 x 9.1 m (30 x 30 ft). Over 90 percent of the seedlings originally planted must be removed, with about five seedlings of the original 50 of each family remaining as crop trees. The first removals were those trees that became diseased by natural infection. Subsequent removals have been based on growth and form, and on family histories of rust resistance. Data on rust infection, height, and growth were taken the third year after planting and every year thereafter. Percent infection data were based on the number of trees of each family within a block that became infected in the field.

## RESULTS

The first loblolly pine seedling seed orchard blocks were planted in 1975 with survivors of greenhouse inoculation tests from 16 wind-pollinated families rated intermediate to good for rust resistance. After 5 yr of exposure to natural field infection, the seedlings in these families ranged from 2 to 56% infection (Table 1). A similar block of slash pine ranged from 21 to 44% infected (Table 2). No susceptible checks were included in the orchard blocks, but adjacent plantings of nursery-run trees had 78% infection at age 5. Therefore, the incidence of rust in the area is moderately heavy.

There was a good correlation ( $r=0.755$ ) between the results from the artificial

inoculation tests and subsequent natural infection on the survivors in the orchard. For example, the first 10 families listed in Table 1 have been consistently among the more resistant in several artificial inoculations, and all of these families had 16% or less infection after 5 yr exposure to natural infection. The next five families have been intermediate in resistance in greenhouse tests and ranged from 18 to 48% infection in the orchard. Family 10-31, the most heavily infected family in the orchard, was a marginal candidate in this planting because in two artificial inoculation tests it had only 25% less infection than susceptible checks.

Mean heights of the tallest 10 trees in each family are shown in Tables 1 and 2. These trees are the most likely to be selected as eventual seed producers. The averages for loblolly families ranged from 4.5 m (14.9 ft) for an open-pollinated family from an Arkansas seed source growing in central Georgia, to 5.7 m (18.6 ft) for another open-pollinated family from Marion County, Florida. The mean height for all loblolly families was 5.0 m (16.4 ft) and the correlation between levels of rust resistance as expressed by percent infection and the mean height of the 10 tallest trees was not significant ( $r=0.185$ ). The mean height for the slash pine families was 4.6 m (15.0 ft), with a range from 4.1 to 4.8 m (13.4 to 15.9 ft).

Since the oldest seedling seed orchard blocks are now only 7 yr old, they are not yet producing many cones, and it is still too early to determine average rust resistance of seedlings from this orchard. Only four open-pollinated loblolly families from the seedling seed orchard have been tested to date, and they had 58% as much infection as the susceptible checks in the inoculation tests, very similar to the maternal parents of these families.

#### DISCUSSION

All of the data from the seedling seed orchard show that survivors from the most resistant families in the artificial inoculation tests also had fewest infections in the field. This correlation, also noted by Dinus and Griggs (3), in-

icates that resistance detected in the juvenile stage is often maintained in older trees under natural conditions. It is also obvious that not all survivors of inoculation tests are resistant in the field, even among the most resistant families. However, individuals selected as final crop trees in the seedling seed orchard will have survived a relatively severe artificial inoculation in the juvenile stage and from 6 to 10 yr exposure to natural infection in the field. They should be some of the most resistant material currently available for breeding programs. Seedlings from these same families have also been planted in survivor progeny tests at several locations. In every case, the survivors from the more resistant families have held up best under field conditions. However, strains of the pathogen that are highly virulent on otherwise resistant selections have been found in specific geographic areas (6), again emphasizing the need for a broad genetic base of resistance.

Many of the progenies initially tested for rust resistance by artificial inoculation were from open-pollinated seed orchard trees. It is likely that the pollen parents of these seedlings were also seed orchard trees with favorable growth characteristics. The remainder of the progenies were from open-pollinated trees in clone banks or progeny tests. The possibility that seedlings in this group have an unselected male parent is higher than for those from seed orchards, but the relatively high intensity of selection practiced in the development of the maturing seedling seed orchard should eliminate the least desirable genetic material while leaving trees with a potentially broader genetic base than those in clonal orchards. The seedling seed orchard approach also avoids some problems inherent in clonal orchards, such as the mechanics of producing grafts, incompatibility, and the adverse effects of the understock on the scion portion of the graft (3). Most important, the seedling seed orchard design is very compatible with breeding programs utilizing survivors of artificial inoculations.

A few forest industries in the Southern U.S. have developed seedling seed orchards, but none designed as a rust resistance orchard, or utilizing survivors of rust inoculation tests. Our orchard is the first of this type. Along with producing resistant seeds, we hope to compare levels of resistance from clonal vs. survivor seedling seed orchards. Eventual production from the entire 24.3 ha (60 acre) seed orchard should exceed 15 million seedlings annually for use in high rust-hazard areas. The test results to date are encouraging, since the relatively few seeds produced thus far in these orchards have produced seedlings with approximately the same levels of rust resistance as their mother trees. These seeds have been produced as the result of pollination from sources outside of the orchard, because very few orchard trees are producing any pollen. As the trees mature and begin producing both male and female flowers, levels of resistance should increase, since the seeds will then be largely from resistant x resistant crosses. In a nearby second-generation slash pine seedling seed orchard established by the Georgia Forestry Commission with full-sib crosses from progeny tested first-generation trees, there was significantly less fusiform rust infection after 4 yr in 16 crosses of resistant x resistant trees than in 17 crosses in which only one parent was classified as resistant ( $P=0.05$ ) (Kraus, unpublished data).

Original estimates of average reduction in incidence of rust from the rust-resistant orchard were 50% for slash pine and 40% for loblolly pine. This estimate is conservative; controlled pollinations of resistant parents indicate that we should produce seeds with more resistance than predicted. Future generations of selections from these orchards should bring the incidence of rust down to less than 33% of that in currently available seedlings.

The most obvious immediate use of the best individuals in the seedling seed orchard would be as new selections to provide scion material for grafting and inclusion in new clonal orchards. In addition, as these trees mature and begin to produce

seeds, their progeny can again be screened for resistance and the cycle repeated with a new generation of survivors.

Since the oldest orchard blocks contain some trees producing cones, limited production should begin within 2 yr. At that time approximately one-half million rust-resistant seedlings will be produced for use in high rust-hazard areas.

#### ACKNOWLEDGEMENT

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Table 1. Fusiform rust infection and height of 16 loblolly pine families in a rust-resistance seedling seed orchard after 5 yr.

Family	Rust infection %	Height <sup>a</sup>	
		(m)	(ft)
SML-9	2	4.7	(15.5)
29-RX1495-35	4	5.0	(16.5)
10-6	4	4.8	(15.7)
TDR	6	5.1	(16.7)
TFS	8	5.3	(17.4)
1495-35	9	4.5	(14.9)
11-9	10	4.8	(15.9)
11-20	11	4.8	(15.8)
42-R	13	4.8	(15.7)
10-5	16	5.5	(17.9)
15-42	18	5.3	(17.3)
2318	28	5.0	(16.4)
T-605	32	5.3	(17.3)
T-601	41	5.7	(18.6)
29-R	48	4.6	(15.0) <sup>b</sup>
10-31	<u>56</u>	<u>5.0</u>	<u>(16.4)<sup>c</sup></u>
$\bar{x}$	19	5.0	(16.4)

<sup>a</sup>Mean height of tallest 10 trees

<sup>b</sup>Based on 6 remaining trees

<sup>c</sup>Based on 9 remaining trees



Table 2. Fusiform rust infection and height of 16 slash pine families in a rust-resistant seedling seed orchard after 5 yr.

Family	Rust Infection	Height	
	%	(m)	(ft)
J-18	21	4.5	(14.9)
2882-23	21	4.3	(14.2)
2905-5	21	4.8	(15.9)
2792-14	21	4.6	(15.0)
2737-11	21	4.5	(14.9)
2797-10	22	4.8	(15.7)
2788-8	23	4.8	(15.7)
2907-5	24	4.7	(15.4)
2882-1	33	4.5	(14.8)
2965-12	35	4.7	(15.3)
3016-1	35	4.6	(15.2)
2972-1	36	4.7	(15.3)
2936-5	41	4.5	(14.6)
86	42	4.6	(15.0)
10-226	43	4.1	(13.4)
3302-21	<u>44</u>	<u>4.6</u>	<u>(15.0)</u>
$\bar{x}$	30	4.6	(15.0)

# The White Pine Seed Orchard Program

in Region One

by

Gerald C. Franc<sup>1</sup>

There are six white pine seed orchards established in Region One, but only two are old enough to produce operational quantities of seed. Those two, the Sandpoint Seed Orchard and the Moscow Arboretum, were established under quite dissimilar conditions and circumstances, and they provide a good opportunity to evaluate white pine seed orchard alternatives.

The Sandpoint Seed Orchard is a grafted orchard made up of 1300 ramets of 13 proven rust-resistant clones. The orchard was established in 1960, using greenhouse grafts. The seed orchard site is within the natural range of western white pine and is itself a white pine site. The seed orchard is adjacent to the Sandpoint Ranger Station and is within the city limits of the town of Sandpoint. The orchard occupies 17 acres and now has about 800 producing trees.

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The white pine arboretum at Moscow was established as a breeding arboretum in 1957 and has been used as a source of seed for reforestation since 1970. The Arboretum is made up of resistant  $F_1$  and  $F_2$  material developed during the research phase of the white pine tree improvement program. Most of the trees were planted as seedlings although some grafts were also included. Over a 10-year period from 1957 to 1967, material was set out in the Arboretum as it became available.

The Moscow Arboretum is on a 25-acre site leased from the University of Idaho. The site is on the Palouse Prairie about 25 miles or so outside the natural range of white pine. There are over 1,400 trees in the arboretum with around 1,200 producing cones.

Neither seed orchard can be considered to be intensively managed. Both received irrigation during the establishment period. The Moscow Arboretum required greater attention during its early years because of the severity of the site. Once the trees became established in each orchard, irrigation was stopped.

A management plan has been prepared for the Sandpoint Seed Orchard, and the responsibility for carrying out the plan has been assigned to the silvicultural staff of the Sandpoint District. Management of the Moscow Arboretum is the responsibility of the Intermountain Station at Moscow.

Ground cover at the Sandpoint Orchard is maintained by mowing. At the Moscow Arboretum, ground cover is controlled by allowing horses to graze the area from early spring until late fall. Grazing was not initiated until the trees were well established and not likely to be damaged by the horses.

Cultural activities including pruning and topping have been carried out at both areas following the procedures recommended by Hoff and Coffen. These cultural activities are designed to improve maintenance and sanitation and to increase cone yield. A copy of their recommendations is attached.

The scion wood used to establish the grafts that were planted in the Sandpoint Seed Orchard came from proven parent trees which were already of flowering age. As a result, small numbers of flowers were produced the first year after planting and in subsequent years. At the same time, very little pollen was produced. For two years, pollen contamination in the orchard was checked by removing what pollen catkins were produced in the orchard and then checking the mature cones for sound seed.

In spite of the fact that all but a very few of the white pine had been removed for one quarter of a mile around the seed orchard, 19 filled seed per cone were counted one year, and 52 seed per cone were found the second year, compared with a normal seed count of 100 seed per cone.

Regardless of the data, concern for contamination was minimal, in part, at least, to the feeling that when abundant pollen is produced within the seed orchard itself, the close proximity of the seed orchard pollen source makes successful pollination by outside sources less likely.

Because of the remoteness from natural white pine stands, pollen contamination in the Moscow Arboretum has not been considered to be a problem.

Graft incompatibility became evident within a few years after the Sandpoint Seed Orchard was established. The problem was so severe that in 1966, five clones with low grafting success were replaced. By 1974, 184 ramets had died. Delayed incompatibility continues to be a problem at Sandpoint.

Because most of the trees in the Moscow Arboretum were established as seedlings, incompatibility is not a consideration.

The trees in the Moscow Arboretum are first and, in some cases, second generation crosses of proven wild parent trees. The grafted trees in the Sandpoint Seed Orchard are equivalent to the wild parent tree and the seed is equivalent to the first generation trees at Moscow. There is an added increment of resistance in each subsequent generation; therefore, the seed produced at the Arboretum has greater resistance to rust than the Sandpoint seed.

Considering that only three years was gained, at most, in the number of years to production in the grafted orchard and since grafting is costly and tends to be a problem due to incompatibility (although this could be minimized by developing compatible root stock) and because an increased level of resistance can be attained by using first generation seedlings as opposed to wild parent scion wood, there is no justification for grafted "First generation" seed orchards in the white pine tree improvement program. Some grafted "advanced generation" seed orchards will be developed from scion wood from outstanding progeny in some older test plantations, however.

Cone production in the Sandpoint Seed Orchard tends to follow that of the natural white pine stands in the area. As a result, the orchard will have bumper years followed the first year by a complete crop failure and then by a gradual buildup to another bumper year.

At the Moscow Arboretum where the trees are offsite, under stress, and stimulated to flower, the fluctuations in the cone crop cycle are less extreme with never a complete cone crop failure. Just the same, best yields at Sandpoint far exceed the best yields at the Moscow Arboretum.

At the Sandpoint Seed Orchard, significant cone losses have resulted from the activities of cone insects. Sanitation by removing all cones from the orchard only temporarily helps to reduce the insect problem since reinvasion of the orchard by cone insects occurs from surrounding natural

stands. Insect control is absolutely necessary at Sandpoint if cone yields are to be maximized, but insecticide use is complicated by the fact that the orchard is within the city and surrounded by human habitation.

Cone loss at the Moscow Arboretum is caused mainly by the severity of the site with a lot of top damage and conelet loss due to wind and snow breakage in the winter. Cone mortality also occurs in July and August due to high temperatures and drought. Irrigation during the summer months would probably greatly increase seed yields.

Cone insects are present in the Moscow Arboretum but at a much lower level than at Sandpoint. Prairie conditions at the Arboretum are less conducive to the insect, and complete sanitation by removing all cones helps to minimize the insect problem.

It is the general opinion among the scientists and tree improvement workers in the white pine program that an intensively managed white pine seed orchard on a natural white pine site, within the range of the species, is most desirable.

Three additional Phase I seedling seed orchards were established from 1971 to 1974. A low-elevation (<3,300 ft.) orchard was established at the Coeur d'Alene Nursery and mid- (3,300 ft. to 4,100 ft.) and high- (4,100 ft.+) elevation orchards were established at the Lone Mountain Tree Improvement Area. These elevational ranges are arbitrary and were established during the early research work in the white pine program.

These three orchards are cultivated and watered as needed and are just beginning to produce significant quantities of cones. The Coeur d'Alene Orchard is the oldest, and small quantities of cones have been collected from it since 1977. Because of low pollen production, all three orchards are mass pollinated with pollen collected from the the Moscow Arboretum.

The so-called Phase II, or operational, white pine tree improvement program was initiated in 1967. The objectives of the Phase II program were to expand the resistance breeding base by selecting additional rust-free trees and to incorporate selection for growth characteristics as well as resistance.

Of significance was the finding by research of very little geographic or elevational variation in western white pine. So strong is the data that it has been determined to eliminate all seed zones for white pine in the Northern Region. As a result, only one Phase II white pine seed orchard is being established.

At the completion of the third rust inspection for each test cycle, selected individuals from those families ranking high in low needle lesion frequency, slow canker development and height growth are lifted from the transplant beds at the nursery and planted at the white pine seed orchard site at Lone Mountain.



Individuals are selected for the following characteristics:

1. No spots resistance
2. Needle shed resistance
3. Fungicidal shoot resistance
4. Bark reaction resistance

In addition, the individuals must be of average or better growth when compared with other individuals in the family block.

There will be about 4 acres of seed orchard established from each cycle of testing. Selected seedlings identified as having a particular resistance mechanism will be planted together in a group so that interbreeding within the group will increase the gain for that particular mechanism. Resistance groups will be planted adjacent to one another with no attempt to minimizing interbreeding between groups and seed from the orchard will be bulked.

The first select Phase II material from test cycles 1 and 2 was transplanted to the seed orchard site in March of 1982.

In addition to the Forest Service seed orchard at Lone Mountain, five seed orchards were established by white pine cooperators from the Cycle 1 and 2 material.

Advanced generation seed orchards are planned utilizing grafts from outstanding individuals from the various Phase I test plantations some of which are 25 years old. This material will be incorporated into the Phase II seed orchard being developed at Lone Mountain. The same procedure will be followed in Phase II test plantations and seed orchards as long-term data on resistance and growth performance become available.

RECOMMENDATIONS FOR MANAGING SEED ORCHARDS  
OF WESTERN WHITE PINE

R. J. Hoff and D. O. Coffen<sup>1/</sup>

A large amount of data has been gathered concerning the production of cones and pollen in the Moscow Arboretum, in the Sandpoint graft seed orchard, and in natural stands.

Based on these data, we recommend the following management practices:

1. Prune trees when the top whorl reaches approximately 10 feet (Figure 1A). Cut the leader off six inches above the whorl (Figure 1B).
2. Each year after, shape trees by removing the terminal bud of any leader showing dominance (Figure 1C). Manage trees to produce 2-3 leaders from the 10 foot height (Figure 1D). The result of pruning will be more cones and pollen and a better shaped orchard tree.
3. Sow grass and keep it close cropped.
4. Water trees when needed. Use a pressure bomb to determine stress and maintain trees at optimal water potential with predawn measurements once a week during dry periods.
5. Fertilize with ammonium nitrate at 300 pounds per acre during late August or early September. Add other elements if deficient.
6. Remove the basal branches to provide fire and rodent protection and to make it easier to move around the orchard with equipment. Remove the bottom two whorls the same year that the leader is cut and remove one whorl per year every 2-3 years thereafter, up to 6-8 feet above ground. The orchard tree should look like Figure 1D 10-15 years after pruning.
7. Harvest cones by climbing the trees and with a mechanical lift such as the "chipmunk."
8. Remove all cones from the orchards each year. This is a sanitation procedure. The purpose is to protect from insects that over-winter in the cones.
9. Collect the following data yearly on each tree, starting the year the tree has been pruned.
  - a. Estimated amount of pollen,
  - b. Counted (when less than 100 cones per tree) or estimated number of cones,
  - c. Cone ripening time.

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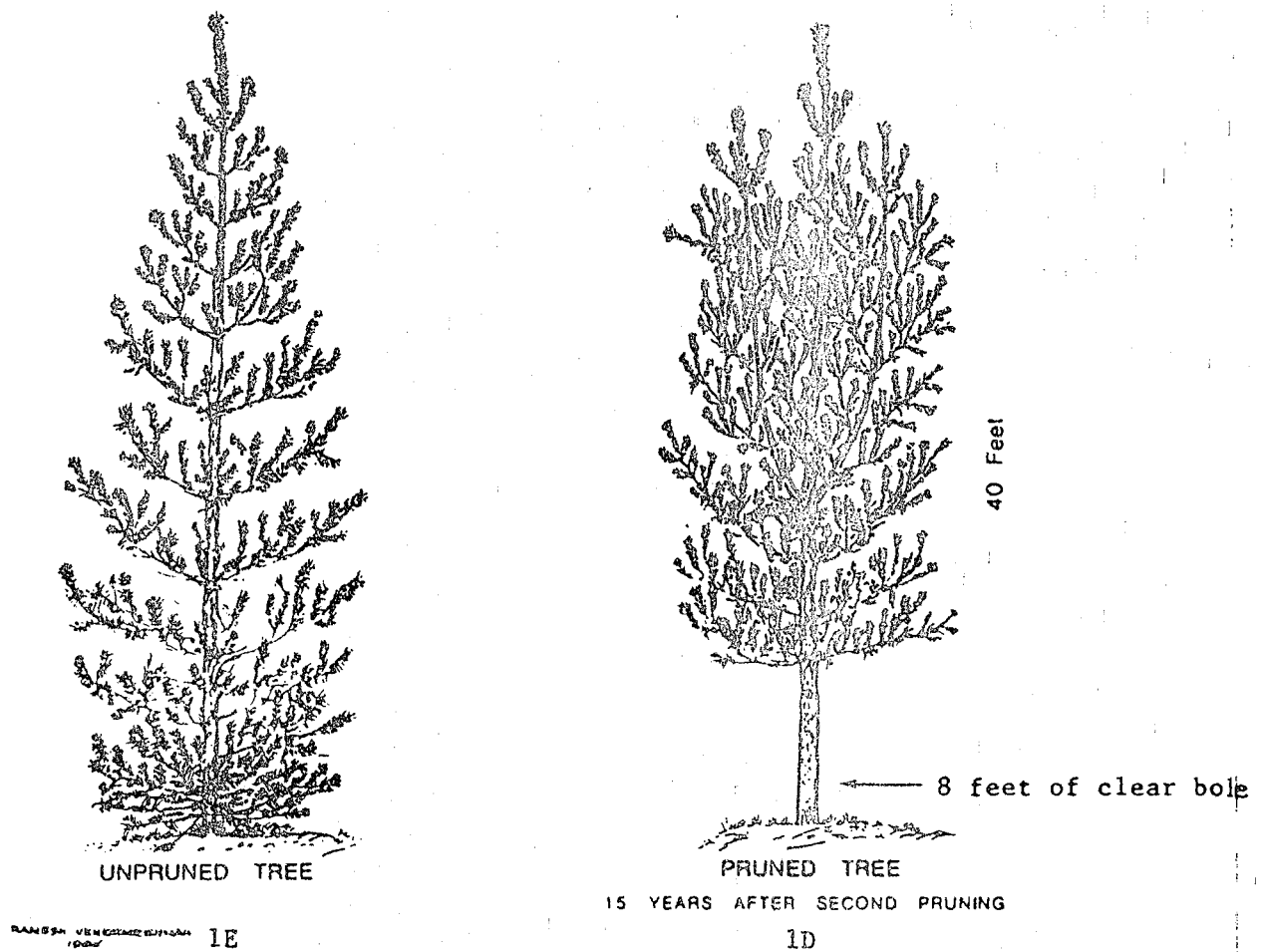
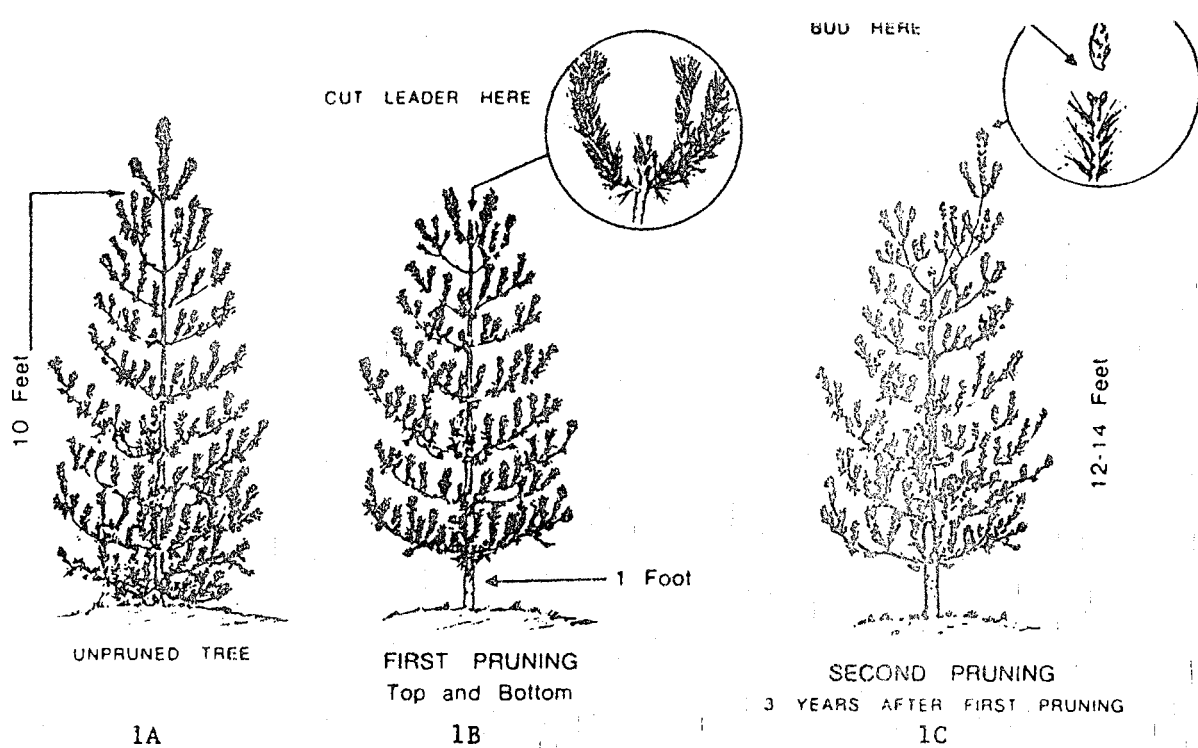


Figure 1.—Method for pruning orchard trees of western white pine for maximum production of cones

Maintaining Genetic Variation in Resistant Populations--  
How Much Variation is Necessary?

Ralph A. Lewis, Forester

I. Introduction

Maintenance of genetic variation has been one of the most intensively studied and widely discussed facets of tree improvement. It is a primary topic of concern among many of the workers and critics of tree improvement and much of this concern centers around the long term ability of our breeding populations to resist the damages of both endemic and introduced forest pests. Virtually everyone agrees that a high degree of genetic diversity should be maintained in a population but the agreement stops there. How much variation is enough and how it will be maintained are questions which have many answers depending on many factors (objectives, scope, resources, etc.) that make up a given breeding program. At the extremes are those who want to be assured that every bit of genetic variation that now resides in a species population will be captured in the breeding program, and those who want to make the highest genetic gain per unit of time with minimal consideration of future diversity. Kleinschmit, (1979) in his discussion of the limitations for restriction of genetic variation, states that "an extreme restriction of the genetic base predisposes a crop to catastrophes. However, an original natural situation can be neither reached today nor has it a biological justification". He lists a number of considerations for genetic variation in forest tree breeding. Among these are:

--Reduction of genetic variation is less dangerous when handling adapted populations than non-adapted ones.

--A reduction of genetic variation is less dangerous the longer a variety has been tested under environmental conditions where the variety will be planted in the future.

--A reduction of genetic variation in the juvenile stage is less dangerous if juvenile-mature correlations are known for their different characteristics.

--Variation finally is based on the genetic structure of a species. Since coniferous species have been found to have high levels of heterozygosity with some loci having 10 or more alleles, it is clear that conservation of a species in a few parent plants is impossible, especially if many alleles (some with low frequencies) are available. Thus, an extreme reduction of the breeding population means a loss of genetic variation and of adaptive potential. On the other hand, it is not necessary to produce all the genotypes in order to conserve the genes.

The literature contains many excellent papers on the subject of genetic variation and disease resistance. Schmidt, Powers and Snow (1981) have provided a broad review of the potentials and needs for genetic diversity in the control of fusiform rust in the southern pines and Hoff, McDonald and Bingham (1976) and Kinloch and Byler (1981) have covered the same topic with white pine blister rust.

This paper will make no attempt to recommend an ideal level of variation either in terms of numbers of individual trees or resistance mechanisms. This does not mean that a decision on the quantity of variation in a breeding program can be avoided. A decision will be made sometime in the program either through a conscious process or by default. For the vast majority of pest resistance problems, we do not have adequate information to make much more than an educated guess but even a guess is better than pure chance.

## II. Basic Principles of Resistance

The following principles of disease resistance are so obvious, they are often ignored or overlooked.

A. Resistance to disease is more common than susceptibility. Most plants are resistant to most diseases.

This is a basic principle that has several important implications. For example, non-host species can be used in place of susceptible host species. Often, a substitution is easier for forest trees than agronomic crops since species with similar product characteristics (wood properties) can be interchanged. Even where susceptible host species are used, non-host species can be used to break up the spatial continuity of the susceptibles.

B. For endemic diseases, there will be significant genetic variation for resistance in the host species population as well as variation in disease incidence due to environmental factors.

In most host species, resistance is usually the rule rather than the exception. If we look at host susceptibility to a rust disease such as fusiform rust, we find that no family (other than suspected hybrids) of loblolly or slash pine is completely resistant but few families are completely susceptible either. Studies of this particular disease indicate that any known resistance in the host species can be essentially overwhelmed by massive inoculation. There are many natural "hot spots" where most of the trees in a given stand are either dead or severely infected by the pathogen. Nevertheless, there are many other portions of the host ranges where the disease incidence is low or even rare. Whether this involves resistance mechanisms directly associated with the host or limitations on the pathogen by other environmental factors is not always clear but the results are similar.

C. Many host organisms are not uniformly susceptible to a disease in all stages of growth and development.

Some diseases affect a host at a certain stage of development while others may affect the plant at any stage. The variation that takes place in growth patterns, environmental influences etc., may be an important source of resistance. It is very important that we recognize that different genes may be active during different stages of the host's development. Each stage may have unique resistance mechanisms in addition to those that are present continuously. Thus, resistance screening should not be limited to a single stage since other factors (both external and internal) may drastically affect the efficacy of these mechanisms.

A simple example would be those resistance mechanisms that do not manifest themselves until a tree is 1-2 years old. If a tree is protected in a nursery with pesticides, that type of resistance mechanism may be effective in protecting the tree after it has been outplanted. On the other hand, that same mechanism may be utterly ineffective if the tree is part of natural regeneration which does not have the benefit of early pesticide protection.

D. All resistance mechanisms that reside in a host population may not have arisen from the classic host pathogen relationship as defined by Flor (1942).

In an unpublished proposition written as a part of his Ph.D. program, at NC State University, Alan Long proposed that the evolution of resistance mechanisms against fusiform rust in pines has not resulted from active "genetic feedback" interactions between host species and the pathogen. Rather, the controlling forces for change have involved a rather passive evolution by the pine host and an active evolution by the rust pathogen to adapt to its alternate host and to regulate its reproductive capacities for a stabilized situation. Thus, the existence of general disease resistance mechanisms and the genes that control these mechanisms may not be due to differential selection pressure by specific races of the fungus but rather the results from the survival value of other metabolic functions of the genes.

Studies by various workers in the South would indicate that there are probably some resistance mechanisms that are racially specific. (Snow and Griggs, 1980; Powers and Mathews, 1980, 1979.) Nevertheless, we should not ignore the facts that there are some good arguments to support Long's hypothesis. Patterns of resistance in loblolly pine as reviewed by Kinloch (1972) and Czabator (1971) indicate that the greatest resistance is found in seed sources from the extremities of the species range--west of the Mississippi and eastern Maryland. This is contrary to most host pathogen systems which have their greatest resistance in the center of the host range. Although several studies (Wells and Wakeley, 1966; Hare and Switzer, 1969; Florence and Hicks, 1980) seem to establish that at least some of this increased resistance is due to introgression of shortleaf with loblolly pine, the high susceptibility in the center of the range tends to suggest that active resistance mechanisms have not been evolved in the loblolly populations.

### III. Genetic Variation

If genetic variation is to provide the primary means of maintaining resistance in our breeding populations, it is not enough to have a large number of trees. Large numbers of individuals often provide a sense of security since there is an assumption that an answer to any problem or condition must be residing in the multitude of genomes. In some cases, this may be a valid assumption but there are important exceptions. Schmidt (1978) points out the classic situation of the American Chestnut (Castanea dentata) and the introduced pathogen, Endothia parasitica, which causes chestnut blight. The host population contained millions of trees that were genetically diverse in virtually every sense of the word except in their ability to resist the pathogen. The population was functionally homogenous in lack of resistance to the disease.

This is an extreme case, but it serves to point out that sheer numbers may mean nothing. Instead, we must look at that variability associated with resistance and specifically at those mechanisms that are effective in resisting the influences of the pest. The genetic variation associated with functional resistance mechanisms constitutes the only meaningful diversity for dealing with the problem. Thus, if we have limited knowledge of the mechanisms, their genetic basis and frequency in the population (which is the normal status of our knowledge for most forest tree pests at this time), there is little that we can do about specifically maintaining genetic variation for resistance in the population. Rather, we are left with the more general task of maintaining genetic variability in the population and hoping that:

- (1) any pest resistance mechanisms that are present in the general population will be represented in the breeding population; and
- (2) Selection pressure for another host trait will not act as a negative selection against any of the important resistance mechanisms. This may have particular importance where the resistance genes are linked tightly to genes controlling other traits or the genes have a more general function than just part of a resistance mechanism.

If we have, or are gaining, some understanding of some of the resistance mechanisms and their genetic basis, we should use that information to insure that effective resistance mechanisms are maintained. This should include all of the identified mechanisms with some priority given to the horizontal resistance mechanisms with multiple gene basis but vertical resistance should not be ignored. Rather we should be emphasizing those mechanisms which have the most promise as "durable" pest resistance. While there is some debate as to the proper meaning of "durable resistance", it appears to be slightly different than horizontal resistance. In a letter to the editor of *Phytopathology* (1981), Roy Johnson of the Plant Breeding Institute, Cambridge defined durable disease resistance as resistance that remains effective while a cultivar possessing it is widely cultivated. He goes on to say that the recognition of resistance as durable does not imply that it will remain permanently effective. The genetic basis for durable resistance may vary and it does not always mean that it is complex. It may not always be equally effective against all races of the pathogen.



#### IV. What Can We Do For The Present?

Obviously, any operational tree improvement program will attempt to maintain genetic diversity in its breeding population for many reasons besides pest resistance. If studies such as those for white pine blister rust have been made which have identified specific resistance mechanisms and their genetic basis (Kinloch and Byler, 1981; Hoff et al, 1976), measures should be taken to maintain a balance of the resistance genes in the population. This does not mean that each mechanism should be equally represented or always represented in all populations but all effective mechanisms should be maintained at a useable level.

If information on specific resistance mechanisms is not available, a more general approach must be taken. Those parents that have demonstrated the ability to produce resistant offspring should be included but it cannot stop there since these trees may have only a few of the potential mechanisms. A wider genetic diversity must be maintained which will contain the potential for producing other forms of resistance.

Maintenance of a broad spectrum of resistance may be purely academic if a wide diversity is being maintained because of considerations other than pest resistance. If the hypothesis is even partially correct that some resistance mechanisms evolve passively as part of other metabolic functions that have a more direct survival role, a significant portion of the potential resistance will be maintained with no direct selection effort.

#### V. What About the Future?

Until more information becomes available for most pest resistance, the operational programs will have to depend upon the more general approaches to maintain genetic variability for resistance. They should be alert for indications of different resistance mechanisms that may show up in early screening or field tests. An example of such indications would be differential reactions to early screening and field testing. One of the most widely known and tested loblolly pine parents in the N. C. State Tree Improvement Cooperative is coded 7-56. In virtually every field test where this parent was represented, its progeny ranked at or near the top in resistance. However, when progeny of this same parent are screening as 4 to 8 week old seedlings, they usually show only intermediate or low resistance. It would appear that at least some of the resistance for 7-56 is based upon mechanisms that do not or cannot express themselves until the tree is more than one year old. Thus, the resistance mechanisms exhibited by 7-56 progeny should be of a different type than those expressed by progeny of other parents that rank high in early screening resistance. Both the resistance shown by 7-56 and that shown by parents in early screening are valuable for maintaining a diversity of resistance mechanisms in the population.

#### VI. Conclusions

1. Based on our current knowledge, it is doubtful if any meaningful number could be assigned as a minimum for maintaining diversity of genetic resistance.

2. More attention needs to be given to the mechanisms of resistance and their patterns of inheritance. Only then will we start to realize the spectrum of variability that resides in a given population and the relative frequency of each defense mechanism.

3. Although we cannot presently define minimum requirements for variability, we do have defacto minimums that are set by our efforts to avoid inbreeding. Until we have a better knowledge of diversity required for resistance, our general efforts to maintain genetic variation will have to serve for maintenance of resistance.

4. Operational programs should be alert for indications of different mechanisms that may reside in their breeding populations. These may provide useful information about the variety and frequency of resistance mechanisms in their breeding populations.

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# RESISTANCE - HAZARD ALIGNMENT: A BLISTER RUST

## MANAGEMENT PHILOSOPHY

by

G. I. McDonald

### INTRODUCTION

White pine blister rust is still a major forest disease problem in the western United States and elsewhere in the world. Longstanding breeding programs have or are nearly ready to produce various types of resistant varieties. It is expected that the causal agent of blister rust (Cronartium ribicola) carries within its genes the capacity to overcome most any single kind of resistance. Therefore, one of the principal objectives of any resistance deployment strategy should be maintenance of genetic breadth in the managed populations of white pines. A simple way to accomplish this objective is to match resistance to an expected level of blister rust hazard. Such a deployment strategy would do three things. First, large tracts of land could be reforested with low-level resistant or susceptible white pines which are readily available and cheaply produced. Second, expensive to develop, highly resistant varieties of white pines could be reserved for those areas that require the sophisticated resistance and could provide the growth to support the extra cost and were not well suited to some immune species. Third, the great genetic breadth maintained should lessen selective pressure on C. ribicola and provide a ready gene pool for future pine improvement programs. The absence of a close adaptation of growth with local environment (Steinhoff 1979) in white pine makes this

an especially attractive strategy. Application of the hazard-alignment deployment method and utilization of a fully integrated, managed philosophy (see McDonald, this meeting) depends on two factors. Can rust hazard be economically measured with enough precision and confidence that forest managers can reliably assess risk and, once measured, will the measurement remain stable or predictable over rotation periods of 50 to 100 years?

Consequently, a quantitative measure of rust hazard was needed. Percent infected was deemed undesirable because it could not account for variation in the time-target relationship. Childs and Bedwell (1948) compared various species of white pines using units of exposure. One unit of exposure equalled one million needles exposed for one year. We reasoned that, since cankers provide a good record of the number of infections a tree accumulates in its lifetime, if one could determine the accumulated amount of target over the exposure period and divide it into the number of cankers accumulated, we would have an index of rust hazard that is independent of time and target size.

#### Pine target model

In the process of developing a computer simulation for white pine blister rust (McDonald et al. 1981), a white pine target model was developed. The ideas of units of exposure, canker accumulation, and the target model were combined to produce a rust hazard index expressed as cankers per thousand needles per year (Fig. 1).

$$\text{RUST INDEX} = R \bar{x}$$

$$R \bar{x} = \frac{\text{NUMBER OF CANKERS}}{\text{SUMMED TARGET}}$$

$$\text{SUMMED TARGET} = \sum_{t=1}^n 8.725 H_t \left( \frac{.45}{H_t^{.75}} + 1.32 \right)$$

= THOUSANDS OF NEEDLES

$n$  = NUMBER OF WHORLS

$H_t$  = TREE HEIGHT AT AGE  $t$

$$= \frac{GI}{0.357 (1.0 - 0.925 e^{-0.20796 A})^{-2.488}}$$

$$GI = H_t 0.375 (1.0 - 0.925 e^{-0.20796 A})^{-2.488}$$

$A$  = TREE AGE (# WHORLS)

Figure 1: Blister rust index models (summed target from McDonald et al 1981; growth index (GI) from Brickell 1970).

This index can be obtained and used in many ways. We are currently suggesting that height, number of whorls, and number of cankers be obtained on 50 evenly distributed crowns in the target stand. Further, these trees should be 10 to 25 years old. The lower limit reflects the minimum exposure time needed to dampen out yearly inoculum density variations, and the upper limit represents a maximum crown size that can be reasonably inspected for cankers. Next, the index is computed for each tree and averaged to provide an index for the stand.

An important question about this index is its stability over time. Factors such as changing climate, changing rust gene frequencies, changing pine gene frequencies, variable age-resistance relationships, and variable inoculum densities could all induce time related changes in the index. An initial look at the stability of the index was obtained from data recorded in 1966 by Region 1. A rust incidence survey was conducted where 84 tree samples were taken from about 150 white pine stands. All 84 trees were inspected in detail for cankers and all cankers were aged. This made it possible to reconstruct the time-infection relationship. Heights were recorded and stand age was determined, which made it possible to reconstruct each year's target amount. In turn, the annual rust index was computed. One stand was 34 years old at inspection and had not received any previous treatment.



The annual index (Fig. 2) for this stand shows exactly the pattern expected from a natural elimination of ribes bushes by stand closure (Moss and Wellner 1953). We see annual variation with a gradual increase up to 19 years, followed by a gradual decrease to apparently complete closure at 30 years.

#### Multiple infection transformation

If the idea of measuring amount of rust in terms of cankers per thousand needles per year is combined with the multiple infection transformation (Fig. 3), one has a way of calculating expected proportion of a stand infected. Given, of course, that the relationship between proportion infected and average number of infections per individual follows the theoretical distribution of random hits.

But, as Fracker (1936) pointed out, a clumped distribution of infection could result from a clumping of ribes bushes. In short, a population might deviate from the theoretical random distribution. Using the canker age data from the stand shown in Figure 2, the actual distribution of numbers of cankers per tree and proportion infected was plotted (Fig. 4). The deviation from the theoretical is considerable. Some possible causes of the discrepancy are ribes bush distribution, variation of wind or other environmental patterns, or variation of host or rust genotype distributions.

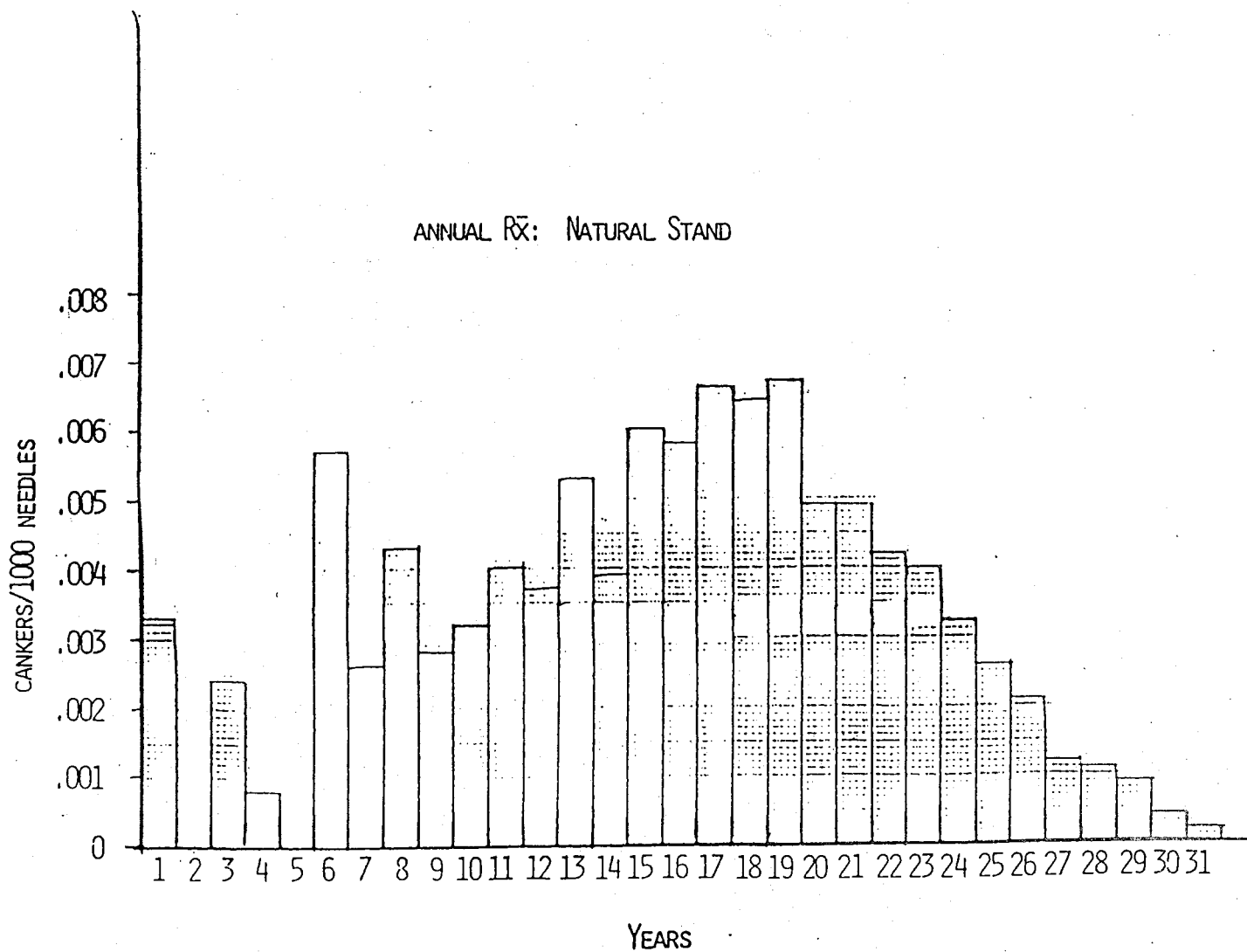


Figure 2. Annual rust index of a 34-year-old stand on the Clearwater National Forest; average of 84-tree sample.

# THEORETICAL MULTIPLE INFECTION TRANSFORMATION

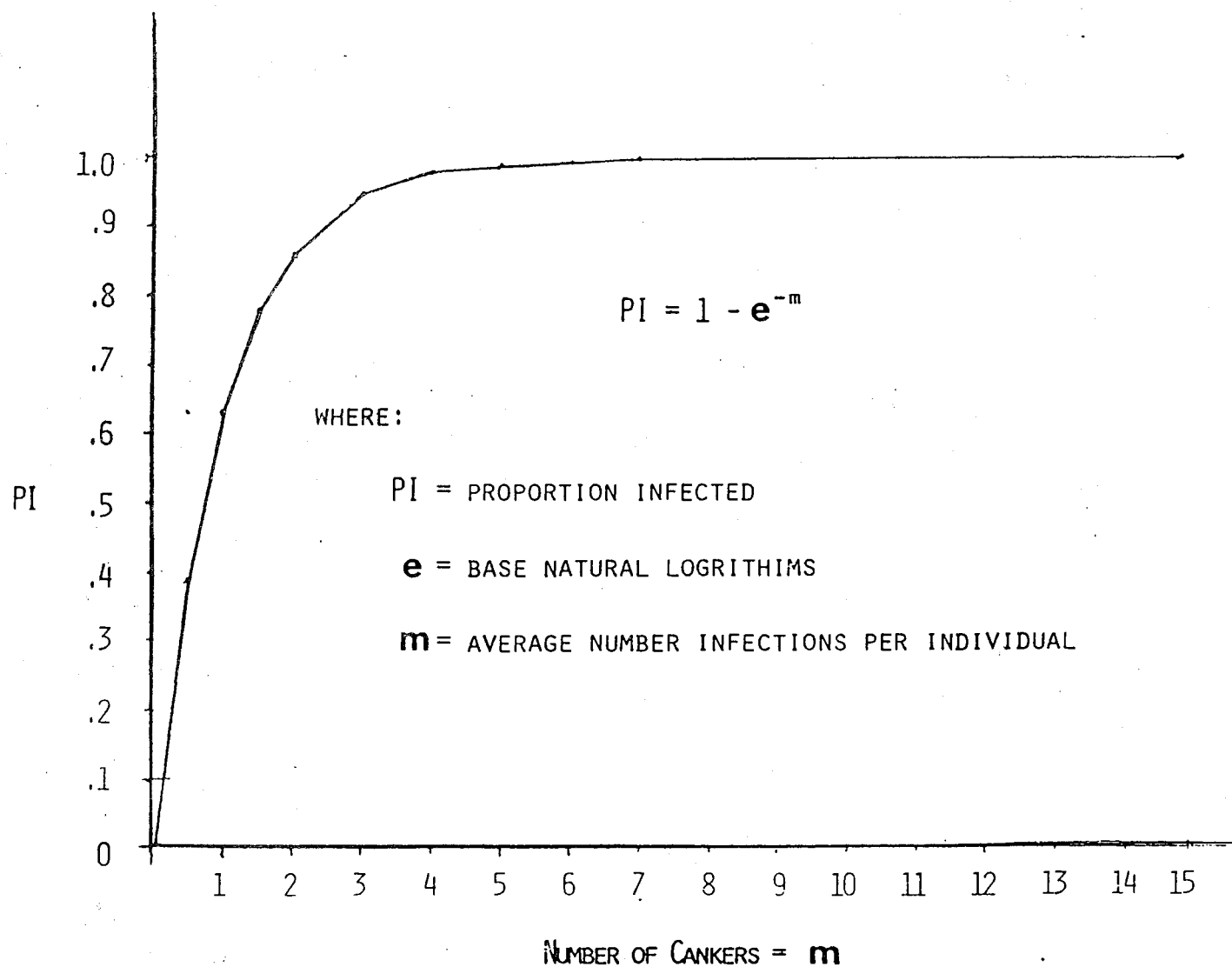
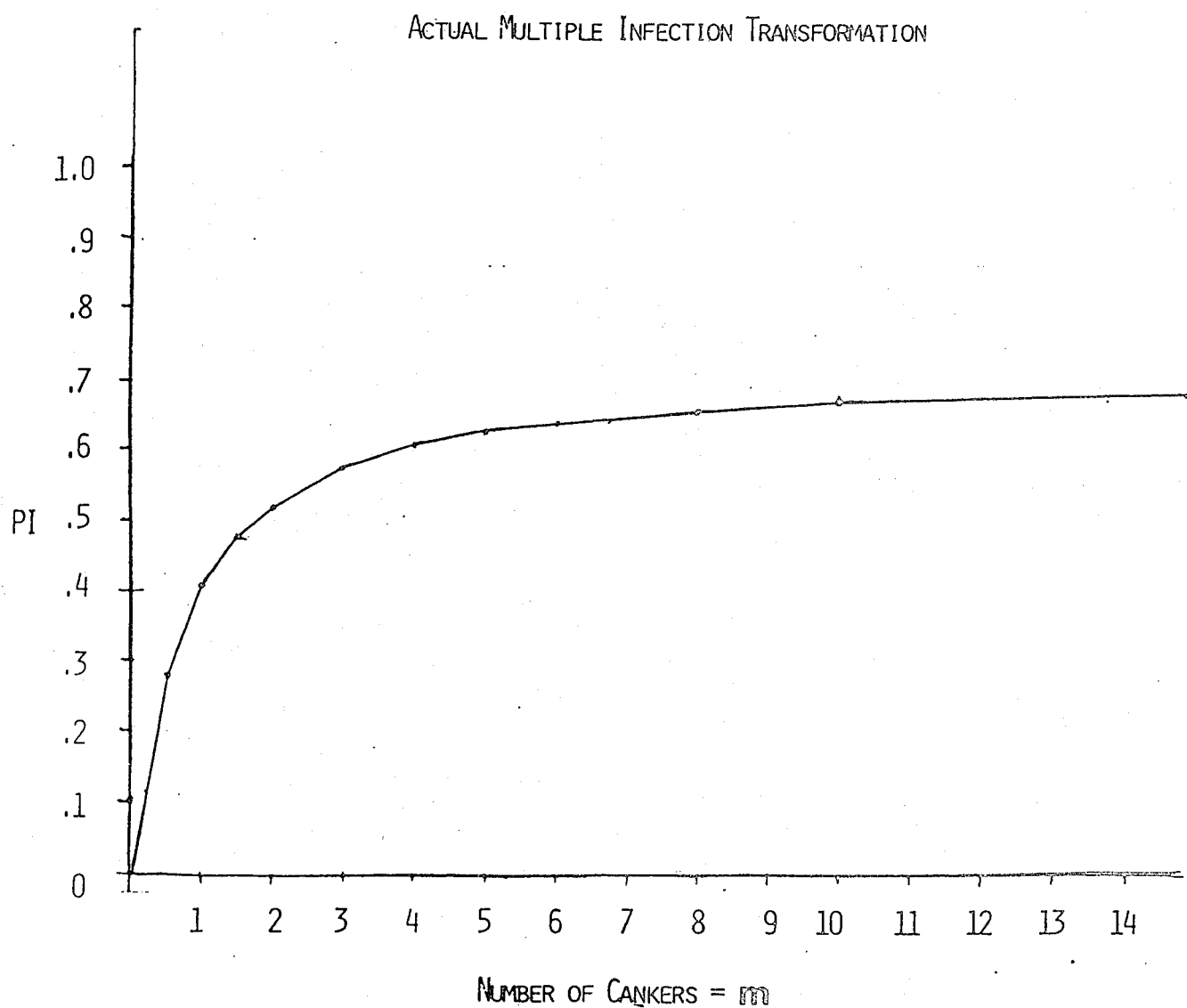


Figure 3. Multiple infection transformation used to relate proportion of stand infected (PI) to average number of infections per individual ( $m$ ) when infection is randomly distributed (from Vanderplank 1975).

Figure 4. Plot of actual probability of blister rust infection as a function of average number of cankers per tree for an 84-tree sample from 34-year-old white pine stand.



One approach to measuring the deviation was suggested by Fracker (1936) in the form of a clumping coefficient. The value 1 and a deviation parameter "d" were added to the exponent of the multiple infection transformation as shown in Figure 5. The resultant equation was solved for d so that two measurable quantities, average cankers per tree and proportion infected (parameters obtained from the 50-tree sample), could be used to assess the deviation present in a particular host population. Values less than 0 indicate a tendency toward a uniform distribution, and positive values of d show a tendency toward an aggregated distribution. Projected performance is estimated as proportion infected as computed by the rust progress model (Fig. 6).

Each descriptor ( $GI$ ,  $R\bar{x}$ , and d) is subject to both environmental and biological sources of variation. The interaction of these sources can be observed by planting populations of known genetic constitution on a variety of sites. The remainder of this paper will deal with the measurement and interpretation of the descriptors for several blister rust resistant white pine populations that have been in the field for up to 22 years.

# MODIFIED MULTIPLE INFECTION TRANSFORMATION

$$PI = 1 - e^{-\left(\frac{m}{1+dm}\right)}$$

WHEN:

$d = 0$  INFECTIONS RANDOMLY DISTRIBUTED

$d < 0$  INFECTIONS TEND TO UNIFORM DISTRIBUTION

$d > 0$  INFECTIONS TEND TO AGGREGATED DISTRIBUTION

$$d = \frac{m - (-\ln(1 - PI))}{m \cdot (-\ln(1 - PI))} = \text{INFECTION DISTRIBUTION FACTOR}$$

Figure 5. Multiple infection transformation modified to account for uniform to aggregated distributions.

# RUST PROGRESS CURVE

$$PI = 1 - e^{-\left(\frac{m}{1+dm}\right)}$$

WHERE:

$$m = R \bar{x} T_t$$

$$T_t = 8.725 H_t \left( \frac{.45}{H_t^{.75}} + 1.32 \right)$$

$t$  = TREE AGE

$H$  = TREE HEIGHT

$R \bar{x}$  = CANKERS/1000 NEEDLES/YEAR

$d$  = INFECTION DISTRIBUTION FACTOR

Figure 6. Rust progress model used to predict proportion infected as a function of 3 epidemic descriptions - growth index (GI), rust index ( $R\bar{x}$ ), and infection distribution factor ( $d$ ).

## Resistance field tests

The resistant populations were created from 1950 to 1970 as outlined by Bingham et al (1960). Three plantations were established in the mid-1950's at Priest River, Deception Creek, and Emerald Creek. These materials contained five stock types representing different levels of selection. Their early performance and a description of the stock types were reported (Steinhoff 1971). The second group of materials contained four stock types planted at Merry Creek and Gletty Creek in 1970 and 1971, respectively. Early results and a description of the plantations were provided by Bingham et al. (1973).

By happenstance the number of cankers per tree, proportion infected, and tree height were recorded in 1970 at Priest River and Deception Creek so that the epidemic descriptors could be calculated at about 12 to 13 years of age at these plantings. In 1981 and 1982, heights and canker counts were made at Merry Creek and Gletty Creek specifically to obtain the descriptors. Both plantations were in their eleventh season when measured. Data from all stock types at each location were combined to produce stock type averages at each site (Fig. 7). The important trends seen in these data are that stock type performance is stable over site, that performance increased with increasing resistance, and that sites can vary a great deal for both descriptors.



# EPIDEMIC DESCRIPTORS

PI = PROPORTION INFECTED

$R \bar{x}$  = CANKERS/1000 NEEDLES/YEAR

**d** = INFECTION DISTRIBUTION FACTOR

STOCK TYPE	PI	R $\bar{x}$	d	PI	R $\bar{x}$	d
	PRIEST RIVER			DECEPTION CREEK		
GCA <sup>2</sup>	.19	.0013	1.65	.29	.0025	1.01
GCA X NON GCA	.23	.0015	1.21	.31	.0028	.86
GCA OP	.33	.0025	.91	.44	.0043	.69
NON GCA OP	.51	.0035	.40	.62	.0066	.30
CONT <sup>1/</sup>	.48	.0038	.64	.69	.0063	.10
	GLETTY CREEK			MERRY CREEK		
GCA <sup>2</sup>	.27	.0026	1.22	.69	.029	.009
GCA X GCA P	.14	.0013	3.69	.71	.0195	.066
(GCA X GCA) <sup>2</sup>	.09	.0012	9.06	.47	.015	.84
CONT <sup>2/</sup>	.82	.015	.31	1.00	.99	.11

<sup>1/</sup> SEED COLLECTED FROM SURVIVORS OF SEVERE EPIDEMICS

<sup>2/</sup> RANDOM WWP SEED COLLECTION

Figure 7. Average epidemic descriptor values for four western white pine plantations.

Some important aspects of stock type comparison are little difference between GCA x GCA and GCA x non-GCA. This means that progeny testing to determine GCA did not result in much increased field performance. One must be tentative on this conclusion because of the limited number of GCA x non-GCA crosses. Another important conclusion is that GCA OP is performing almost as well as GCA x GCA. This means that OP seed could be collected from progeny-tested wild parents with little loss in resistance performance but with a large gain in genetic breadth. Likewise, backcrosses to the GCA parents from the GCA x GCA selected populations performed almost as well as the second generation materials (GCA x GCA) x (GCA x GCA). It is interesting to note that the backcrosses and second generation materials showed nearly equal Rx values but considerably different d values.

Data shown in Figure 7 can be integrated over all stock types by calculating improved/wild ratios for each descriptor. We have assumed for the time being that the ratio for Growth Index is 1. Figure 8 provides descriptors relative to wild seedlings and expected performance on 9 presumed sites varying in hazard from very high to very low. But proportion infected is not the most relevant measure of performance. A mortality prediction would be of much more value.

# EXPECTED PI AFTER 40 YEARS

STOCK TYPE	IMPROVED/ WILD		d = .1					d = .2				d = .75			
			R $\bar{x}$ =					R $\bar{x}$ =				R $\bar{x}$ =			
	R $\bar{x}$	d	1.0	.5	.005	.0005	.00005	.5	.005	.0005	.00005	.5	.005	.0005	.00005
WILD SEEDLINGS	1.0	1.0	1.0	.99	.99	.90	.33	.74	.73	.64	.28	.74	.73	.64	.28
NATURAL SELECTION OP	.47	1.0	1.0	.99	.98	.72	.18	.74	.71	.56	.16	.74	.71	.56	.16
NON GCA OP	.46	1.1	1.0	.99	.98	.75	.18	.70	.68	.53	.16	.70	.68	.53	.16
GCA OP	.32	2.5	.98	.86	.83	.56	.12	.41	.40	.32	.12	.41	.40	.32	.12
NON GCA X GCA	.20	3.2	.96	.79	.74	.43	.08	.34	.33	.28	.10	.34	.33	.28	.10
GCA <sup>2</sup>	.17	4.0	.92	.71	.70	.37	.07	.28	.27	.21	.06	.28	.27	.21	.06
GCA <sup>2</sup> X GCA P	.10	10.0	.63	.39	.36	.21	.04	.12	.12	.10	.03	.12	.12	.10	.03
(GCA X GCA) <sup>2</sup>	.09	30.0	.28	.15	.15	.11	.03	.04	.04	.04	.02	.04	.04	.04	.02

Figure 8. Relative epidemic descriptor values for western white pine stock types and their expected performance after 40 years' exposure to 9 different combinations of R  $\bar{x}$  and d representing 9 sites.

### Mortality in field tests

There should be a strong relationship between PI and mortality. Such appears to be the case as shown by the 22-year results from the Priest River, Deception Creek, and Emerald Creek plantations (Fig. 9). The ratio of proportion dead rust:proportion infected seems to be quite uniform over sites and stock types at .3. All sites have about the same degree of hazard and the same exposure time.

# MORTALITY VS PROPORTION INFECTED

V-Q PLOTS 22 YEARS

STOCK TYPE	PR			EC			DC			$\bar{x}$
	PI	PDR	PDR/PI	PI	PDR	PDR/PI	PI	PDR	PDR/PI	
GCA X GCA	.32	.10	.31	.46	.17	.37	.35	.12	.33	.34
GCA X NON GCA	.38	.07	.18	.43	.13	.30	.39	.15	.38	.29
GCA OP	.45	.11	.24	.58	.20	.34	.55	.20	.36	.31
NON GCA OP	.75	.15	.20	.74	.15	.20	.74	.30	.40	.27
CONT	.68	.20	.29	.86	.28	.33	.81	.27	.33	.32
$\bar{x}$			.24			.31			.36	.31

Figure 9. Ratio of blister rust mortality to proportion of trees infected with blister rust for 5 western white pine stock types growing at 3 sites in northern Idaho; PR = Priest River Experimental Forest; EC = Emerald Creek; and DC = Deception Creek.

The other two plantations show a somewhat different pattern (Fig. 10). These plantations were not only younger (11 years' exposure), but the hazards vary widely from about .01 to 1. The Gletty Creek site is comparable to the three older sites, and we can assume that the PDR/PI ratio will be about .3 at 20 years. We can also assume that the wild seedlings will give a ratio of 1 by 20 years. It is expected that the resistant materials at Merry Creek will stabilize at about .8 or .9. If the relationship between the PDR/PI ratio and Rx is linear, then we would expect the ratio for susceptible material to be given by

$$\text{PDR/PI wild seedling} = .7 \text{ Rx} + .3$$

and

$$\text{PDR/PI resistant seedlings} = .5 \text{ Rx} + .3.$$

Using the above linear equations, we can translate the PI values in Figure 8 to PDR given in Figure 11. If an arbitrarily chosen mortality level of .25 at 40 years is used then the table can be partitioned into acceptable and unacceptable combinations of material, susceptible to highly resistant, and hazard.

# MORTALITY VS PROPORTION INFECTED

## PILOT RESISTANCE PLANTATIONS -- 11 YEARS

STOCK TYPE	GLETTY CREEK			MERRY CREEK		
	PI	PDR	PDR/PI	PI	PDR	PDR/PI
GCA X GCA	.27	.05	.19	.69	.56	.81
GCA X GCA P	.14	.03	.21	.71	.44	.62
(GCA X GCA) <sup>2</sup>	.09	.004	.04	.47	.40	.85
CONT	.82	.08	.10	1.00	.996	.996

Figure 10. Ratio of blister rust mortality to proportion of trees infected with blister rust for 4 types of western white pine stock growing at 2 sites in northern Idaho.

# EXPECTED MORTALITY AFTER 40 YEARS

STOCK TYPE	IMPROVED/ WILD		$d =$					$d = .75$			
	$R\bar{x}$	$d$	$d = .1$	$d = .2$				$d = .75$			
				$R\bar{x} =$				$R\bar{x} =$			
	$R\bar{x}$	$d$	1.0	.5	.005	.0005	.00005	.5	.005	.0005	.00005
WILD SEEDLINGS	1.0	1.0	1.0	.64	.64	.27	.10	.48	.22	.19	.08
NATURAL SELECTION OP	.47	1.0	.80	.54	.30	.22	.05	.41	.21	.17	.05
NON GCA OP	.46	1.1	.80	.54	.30	.22	.05	.39	.21	.16	.05
GCA OP	.32	2.5	.78	.47	.25	.17	.04	.23	.12	.10	.04
NON GCA X CGA	.20	3.2	.77	.43	.22	.13	.02	.19	.10	.08	.03
GCA <sup>2</sup>	.17	4.0	.74	.39	.21	.11	.02	.15	.08	.06	.02
GCA <sup>2</sup> X GCA P	.10	10.0	.50	.21	.11	.06	.01	.07	.04	.03	.01
(GCA X GCA) <sup>2</sup>	.09	30.0	.22	.08	.05	.03	.01	.02	.01	.01	.01

Proportion Dead from Rust =  $PI (.5 R\bar{x} + .3)$  for Resistant seedlings

=  $PI (.7 R\bar{x} + .3)$  for Wild seedlings

Figure 11. Predicted mortality of 8 types of western white pine stock on 9 levels of rust hazard assuming ratio of improve/wild GI to be 1 and GI = 90. Body of data divided into acceptable and unacceptable combinations on basis of .25 mortality at 40 years.



## CONCLUSION

Thus, hazard-resistance alignment would work by measuring the relative descriptors for each seed source and then predicting performance on the basis of site-specific descriptors where planting was contemplated. One must keep in mind, however, that logging practices and Ribes ecology can interact to cause explosion of Ribes plants after a site has been indexed. Any application of this method should also provide for expected changes in ribes population. If experience and further testing show that the indexing approach is consistent and workable, we will have available a management technique that would enable safe planting of low-level resistance; reservation of expensive, highly resistant, and genetically restricted seed for plantations where it is really needed; and, at the same time, greatly expand the pine gene pool with all the concomitant positive aspects. Finally, this approach to deployment of resistance revolves around an index of rust hazard that also can be the quantitative measure of rust serving as the fundamental tool for overall integrated rust management (McDonald, this meeting).

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Rating Forest Stands for Disease and Insect  
Damage Potential in the Pacific Northwest

By

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In treating human diseases, doctors fit the medication to the severity of the illness and size and age of the patient. Forest pest managers are moving in the same direction by fitting the treatment to the severity of the pest threat. Forest stands are being rated for their susceptibility to pests. The damage likely to result from these pests is being predicted. The objective of forest pest risk rating systems is to match forest pest management strategies to the amount of resource damage anticipated if no control actions were to be undertaken. An example will illustrate my point. Clearcutting is a biologically effective method of controlling dwarf mistletoe; however, if in a young plantation only one tree per acre is infected, clearcutting the plantation would not be an appropriate treatment, whereas cutting the one infected tree per acre would be because the short-term risk is still confined to the one tree per acre. Risk rating stands for pests should help us move away from crisis management where we rush from outbreak to outbreak. Risk rating should enable us to devise and implement appropriate strategies to prevent many outbreaks.

Risk rating stands for pest damage has been practiced for many years in the Pacific Northwest. However, until very recent times, usually only stands that were already infested were risk rated. Also, the risk rating tended to yield qualitative and not quantitative results. In the last few years, pathologists, entomologists, and their associates in the Pacific Northwest have been able to utilize risk-rating systems that predict, in numerical terms, losses that are likely to occur from a few of the major pests.

In the mid-1960's the practice of *Ribes* eradication as a method of controlling white pine blister rust was stopped on Federal lands in Oregon and Washington. This decision was based upon results from many surveys of individual white and sugar pine stands where *Ribes* eradication work had been performed. In many of these stands it was discovered that *Ribes* eradication was not effective in controlling the disease. The main thrust in controlling white pine blister rust was shifted to selecting trees with resistance to the disease.

In the western white and sugar pine-growing areas of Oregon and Washington, the extent of white pine blister rust varies tremendously. The reason is largely due to climatological differences from location to location. There are some areas such as the Warner Mountain Range near the south-central town of Lakeview, Oregon where, because of low rainfall and low relative humidity, white pines rarely become infected. At other sites, particularly at higher elevations within the Cascade Mountain Range, white pine blister rust infection can occur every year. Differences in *Ribes* species and population numbers from location to location also influence the amount of infection.

A combination of four factors has prompted the Forest Service to initiate efforts to match western white and sugar pine management to white pine blister rust hazard. These factors are: (1) a variation in infection hazard from location to location; (2) increasing availability of resistant planting stock; (3) awareness of the McDonald hazard rating system used in the Northern Region; and (4) the desire of Oregon and Washington foresters to actively manage western white and sugar pine.

White pine blister rust hazard rating is in its infancy on Federal lands in Oregon and Washington. No sites have yet been operationally rated for rust hazard, but the groundwork is being laid. A two-level approach is being planned.

The first or broad-level approach will attempt to hazard rate entire tree seed zones. These zones are large areas that may encompass as much as one-half million acres. The seed zones will be categorized as low, medium, and high hazard. The seed zone approach is being taken to help us identify locations where we need to do more intensive, site specific evaluations, namely the high- and medium-hazard areas. The seed zone approach will enable us to develop a priority list for site specific evaluations. The system presently being evaluated uses only weather data for a 10- to 20-year interval. Point source historical weather data from locations within the seed zones of interest are computer accessed to identify any episodes when 0.30 inch of rainfall occurs in a 1- or 2-day span from August through October--the time of pine infection. The ratings are being checked by hazard rating individual stands within the seed zones and by reviewing whatever rust incidence data are available in existing records, such as aerial surveys. We also plan to evaluate hazard rating of seed zones by using the computer simulation program developed by McDonald, Hoff, and Wykoff. We fully understand there could be wide variation in rust infection hazard within different sites in a tree seed zone. The tree seed zone approach is not intended to be used for site specific treatments.

The second level of hazard rating takes place at the individual stand level. The system developed by McDonald for use in western white pine stands in the Northern Region is being used, so far with no modifications, in Oregon and Washington. Fifty- to one-hundred pines ranging from 10 to 25 years old are examined for rust infections. No sugar pine stands have been rated; however, we intend to try a few this fall.

It is difficult to hazard rate some stands of interest because there are either no pines present since they all died, were harvested, or if they are present, are too large to use the McDonald system. In such cases, nearby sampleable stands could be used as proxies or the seed zone hazard rating may be used. Another approach being used is to examine the sites for numbers and species of *Ribes*. Some *Ribes* species are not good carriers of the blister rust.

The purpose of white pine blister rust hazard rating is to relate the intensity of rust management practices to the damage anticipated if no control actions are taken. In high-hazard areas, we would expect to plant only progeny of pines that show high levels of resistance or not manage for pines. In medium-hazard zones, planting of pine stock with lower levels of resistance may be appropriate. *Ribes* population reduction may be undertaken in some medium hazard sites as well as lower branch pruning. On low hazard sites, blister rust would be virtually ignored except for occasional monitoring. Progeny from nonresistant parents could be planted in low hazard areas.

White pine blister rust is not the only pest for which forest stands are hazard rated in the Pacific Northwest Region. Laminated root rot caused by *Phellinus weirii*, is one of the most common root rots in this Region. Susceptibility varies widely among tree species. It is possible to predict the hazard in infected stands based upon tree species present. Forest pathologists routinely recommend laminated root rot hazard be reduced by favoring less susceptible tree species such as pines or hardwoods. A model developed by the Canadian Forestry Service will predict losses over time in infected stands.

Decay hazard to true fir stands by the fungus *Echinodontium tinctorium* can be predicted by age and degree of suppression of existing true fir understories and presence of conks in overstory trees. This information is being used to decide if existing true fir understories are manageable or if they should be eliminated because decay losses would be too large if the stands were carried to normal rotations.

Technology is available to hazard rate stands for Douglas-fir tussock moth damage, but is presently not being widely used in the Region.

Lodgepole and ponderosa pine stands are being rated for susceptibility to damage by mountain pine beetle. This information is being used to schedule thinning and harvest operations to prevent unacceptable losses.

In summary, hazard rating forest stands for pest damage potential has been done for several years in the Pacific Northwest. Recent efforts on a few of the major pests have resulted in quantitative loss predictions. Forest pest hazard rating enables forest managers to align forest pest management strategies with anticipated damage.

## RATING SITES FOR FUSIFORM RUST HAZARD AND TREES FOR RUST RESISTANCE

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Abstract.--The percentage of trees infected by fusiform rust varied considerably during the first five growing seasons in nine plantations of slash pine. Some plantings developed over 50 percent infection in 3 years; others, in only 1 or 2 years; and one plantation developed less than 20 percent infection in each year. Frequency of heavy infection is believed to be the only reliable criterion for assessing site hazard to fusiform rust. Probabilities of a tree becoming infected for the first time in the fifth growing season was surprisingly high, even in plantations with more than 50 percent cumulative infection after four seasons. In all plantings, probabilities of reinfection in the fifth season were consistently higher than probabilities of first infection. Shoot phenology and development are believed to be major factors controlling fusiform rust infection in any one night, season, or sequence of growing seasons.

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Fusiform rust of southern pines is similar in many respects to blister rust of eastern and western white pines. Both diseases are caused by fungi of the genus Cronartium (C. quercuum (Berk.) Miyabe ex Shirai and C. ribicola (Fisch.)). These fungi require alternate hosts to complete their life cycles (oaks and ribes), and both cause tree mortality and deformity. Several differences exist between the diseases. White pine blister rust was introduced into the United States, but fusiform rust is considered indigenous to this country. White pines are subject to serious damage even when they reach sawlog size, while fusiform rust seems to be much less damaging when infections occur after the first several growing seasons. Another difference is that blister rust is a serious problem in natural stands as well as plantations, but fusiform rust is most

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damaging in pine plantations although old-field type natural stands also may be heavily damaged.

In 1974, Glenn Snow and I established a field study to relate incidence of fusiform rust to climate, inoculum, and other factors. The three coastal counties of Mississippi were chosen for study because incidence of disease had been shown to range from 2 to 80 percent in unthinned plantations of slash (Pinus elliottii Engelm.) and loblolly pine (P. taeda L.). This distribution of rust is shown in Figure 1, and our nine study areas were selected intentionally to try to encompass a range of disease hazards. We planted each of the nine areas with 750 trees of three slash pine sources. One source was derived from a seed orchard established for improved growth and rust resistance. The other two sources, from two different state tree nurseries, were not considered resistant to fusiform rust.

In 1974 through 1981, complete records were kept of every stem infection and most branch infections on every tree. Observations included years of gall origination, the distance above the ground and to the main stem, the year branch galls grew into main stems, and the year that the gall or tree died. The first objective of this paper is to discuss procedures for rating sites to fusiform rust hazard. A second objective is to discuss factors that influence disease escape, a topic of importance to the selection and breeding of trees with resistance to fusiform rust.

#### Identifying high hazard sites for fusiform rust

The first and third growing seasons were very light infection years over the entire Gulf Coast area. However, infections varied considerably from site to site in the second, fourth, and fifth seasons (Figure 2). Plantings 2 and 8 were heavily infected in all three of the heavier rust years. Plantation 1 and



9 were moderately infected in the second and fourth seasons but heavily infected in the fifth. Plantations 3, 4, and 5 were very lightly infected through the fourth season, but infection was heavy in the fifth. In the second season, infection was heaviest of all in plantation 7, but infection was light in the fourth and moderate in the fifth. Plantation 6 was the only plantation to escape moderate or heavy infection in all years. We had not anticipated this variability in infection and it clouded our concept of low and high hazard sites for fusiform rust. The "resistant" source may be slightly less infected overall, but the differences were small and inconsistent among plantings and years (Figure 2). Therefore, the use of three seed sources did not affect the perspective of relative hazard between plantings.

When cumulative infection is viewed after the fourth or fifth season, a completely different perspective of hazard is obtained (Figure 3). After the fifth season, cumulative infection was very high in eight of nine plantings. However, if the plots were examined today, planting 7 would appear to be most heavily infected because trees developed many galls and severe deformities during the second season; many trees have already died. If infection had occurred in the fifth season instead of the second, as in plantations 3, 4, and 5, a totally different impression of hazard would be obtained. The impressions of hazard also would be reversed if heavy infection had occurred in the second season in plantings 3, 4, and 5. Most of that infection is confined to branches.

From these data we conclude that site hazard must be considered in terms of probabilities, similar to the recommendation of Large (1966) that hazard be expressed as the number of years out of 10 in which heavy damage has occurred. Large's recommendation for diseases of agricultural crops offers reasoning patterns for forest diseases. When heavy infection in a plantation can be

attributed to infection that occurred only during a single growing season, as in plantations 3, 4, and 5, that planting may still be considered low hazard for fusiform rust. Only when heavy infection occurs in two or more years is it probably safe to conclude that the area is high risk to disease. Similar multiple infection years in several nearby plantings of different age classes would increase the probability that the area in question is high risk to fusiform rust.

#### Selecting for disease resistance.

One approach used by the earlier breeders was to develop grafted seed orchards from scion material collected from disease-free "super" trees in natural stands of slash pine. Many of the very early selections looked very promising when tested against artificial inoculum or in the field. However, when Goddard et al. (1975) performed field progeny tests, they found that the levels of infection varied according to selection pressures that the original parents had encountered. The parents of population A were disease-free trees located in natural stands with low levels of fusiform rust. Progeny of population A experienced more infection in three test plantings than population B, whose parents were the residual disease-free trees of a 10-acre pine plantation which, once having more than 90 percent infection, was then rogued of all infection and converted to a seed orchard. Goddard concluded that very little gain in resistance can be expected unless parent trees are chosen from areas of heavy selection pressure for fusiform rust. It is not surprising, therefore, that the seed source selected for resistance in our study did not perform any better than the other sources. The parent trees used to develop the orchard were similar to the parents of population A of Goddard, and the progeny test rankings were based on field trials where levels of infection did not exceed about 50 percent.

A rather sizeable collection of slash pine families exists in various seed orchards throughout the South. Some were chosen from parent populations where the selection pressure from fusiform rust was not great. Others are more typical of the families of Goddard's population B which had been subjected to more demanding pressures. The prevailing feeling is that considerable gain is imminent with current seed orchard selection. Actual gains are difficult to judge because 1) progeny tests often have not been conducted on sites that developed heavy infection, 2) experimental designs, by necessity, are often unbalanced and the same families are not planted on every site, and 3) sources used as experimental checks vary from one experiment to another. When Goddard et al (1975) compared population A, representing low selection pressure, with population B, representing high selection pressure, 21-27 percent less infection was noted in population B on the three highest incidence plantings. However, when Goddard and Schmidt (1979) made further selections from population B and compared their performance in nine plantings to known susceptible checks, differences may have been actually less than the previous population A vs B comparisons.

In our study, we had assumed that the population of trees which had escaped infection through the first four growing seasons possessed a high degree of resistance to fusiform rust. In plantation 2, however, with 59 percent infection through 4 years, a surprising 69 percent of the disease-free trees became infected for the first time in the fifth season (Figure 4). A high percentage of disease-free trees also were infected for the first time in several other plantings. Nevertheless, the probabilities for reinfection were consistently higher than probabilities for first infection. When the data of Figure 4 were analyzed by seed source, probabilities for reinfection were consistently high among all seed sources only in plantings with more than 40 percent cumulative

infection through four seasons. Thus, the differences expressed in Figure 4 for plantings 3, 4, 5, and 6 may not be significant even though they fit the general pattern.

The disease-free trees after five seasons in plantations 2 and 8 were probably comparable to the disease-free trees of population B described by Goddard et al (1975). Why have they not become infected? Many factors govern fusiform rust infection. In 1978, some individual trees in our study were infected with as many as 50 galls, while adjacent trees escaped infection completely. Even in years or sites with low infection, it was common to find multiple infections on individual trees and it is difficult to conceive that any tree did not receive adequate inoculum to infect it. However, during the course of our investigations, it has become increasingly clear that shoot phenology and development must play a very important role in the susceptibility of trees to fusiform rust. Very often infection occurred on exactly the same relative positions on branches, indicating that infection probably occurred on the same night. During a growing season, individual trees of the same age class vary considerably from week-to-week in shoot tenderness, shoot length, needle length, timing of flushes and general appearance. These characters also vary between branch whorls of individual trees. Whether a tree becomes infected on a single night, a growing season, or over several seasons therefore seems to be controlled to a large degree by coincidences of inoculum, favorable weather, and tissues susceptible for infection. Thus, many current selections from high hazard sites may have escaped infection because shoot tissues were not susceptible to infection at times when other factors were favorable.

Further research seems warranted to resolve the factors that control susceptibility to fusiform rust. What roles do shoot phenology and development have

on infection? If these traits prove important, can they be instrumental in tree improvement programs?

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## FIGURE CAPTIONS

1. Incidence of fusiform rust (percent branch or stem cankered trees) in unthinned slash or loblolly pine plantations ranges from about 2 to 80 percent in south Mississippi. Nine areas planted to study the causes of this variation are indicated.

2. Percent of trees infected with fusiform rust in each of the first five years after planting. Nine plantations and three seed sources are shown. The center bar is a seed source which was believed to possess some resistance to fusiform rust.

3. Percent cumulative infection in nine plantations after the second, fourth, and fifth growing seasons. The center bar is a seed source which was believed to possess some resistance to fusiform rust.

4. Percent of trees infected with fusiform rust in the fifth growing season. The bars on the left represent trees infected sometime prior to the fifth season, but the trees shown by the right bars were not infected before the fifth season.

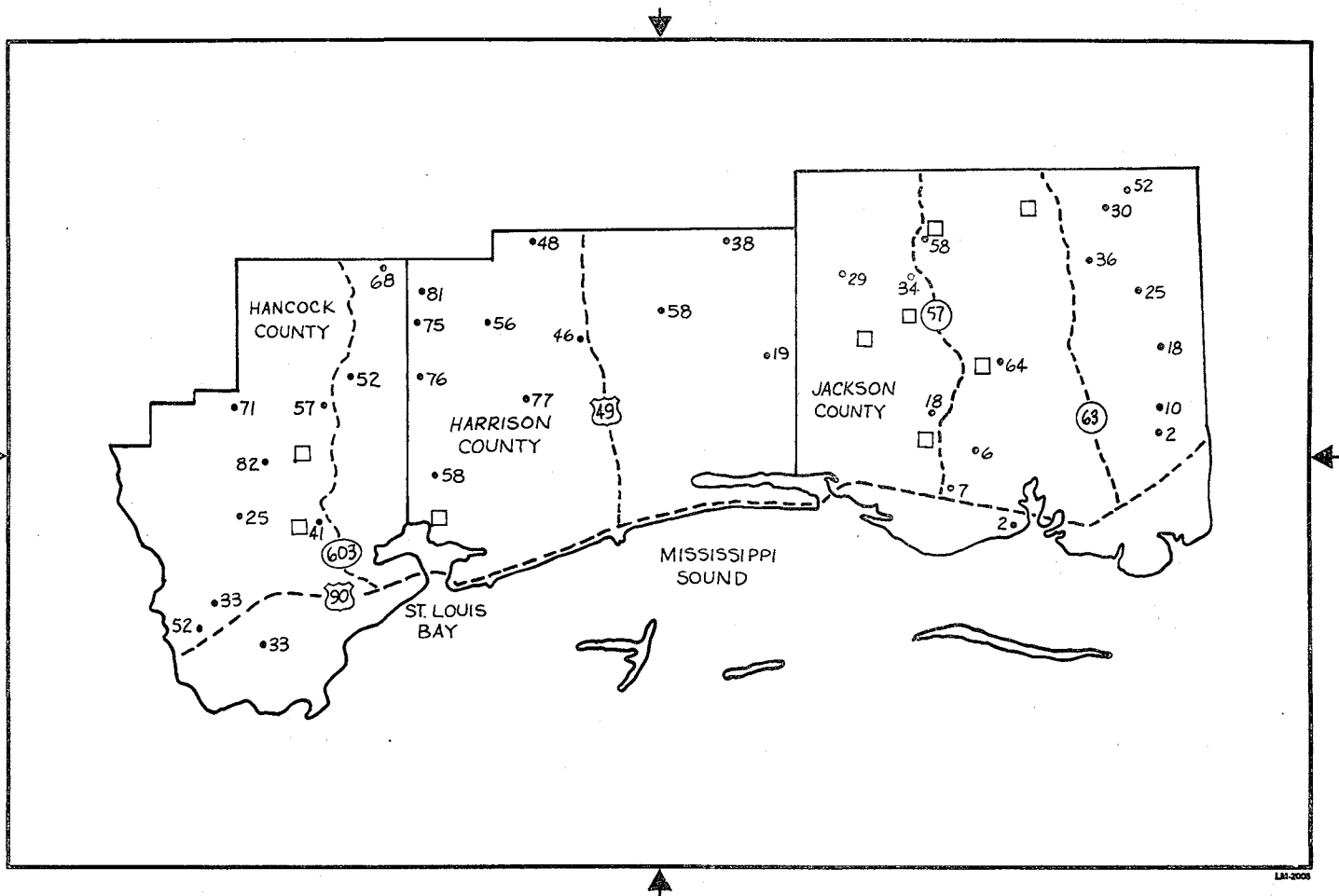


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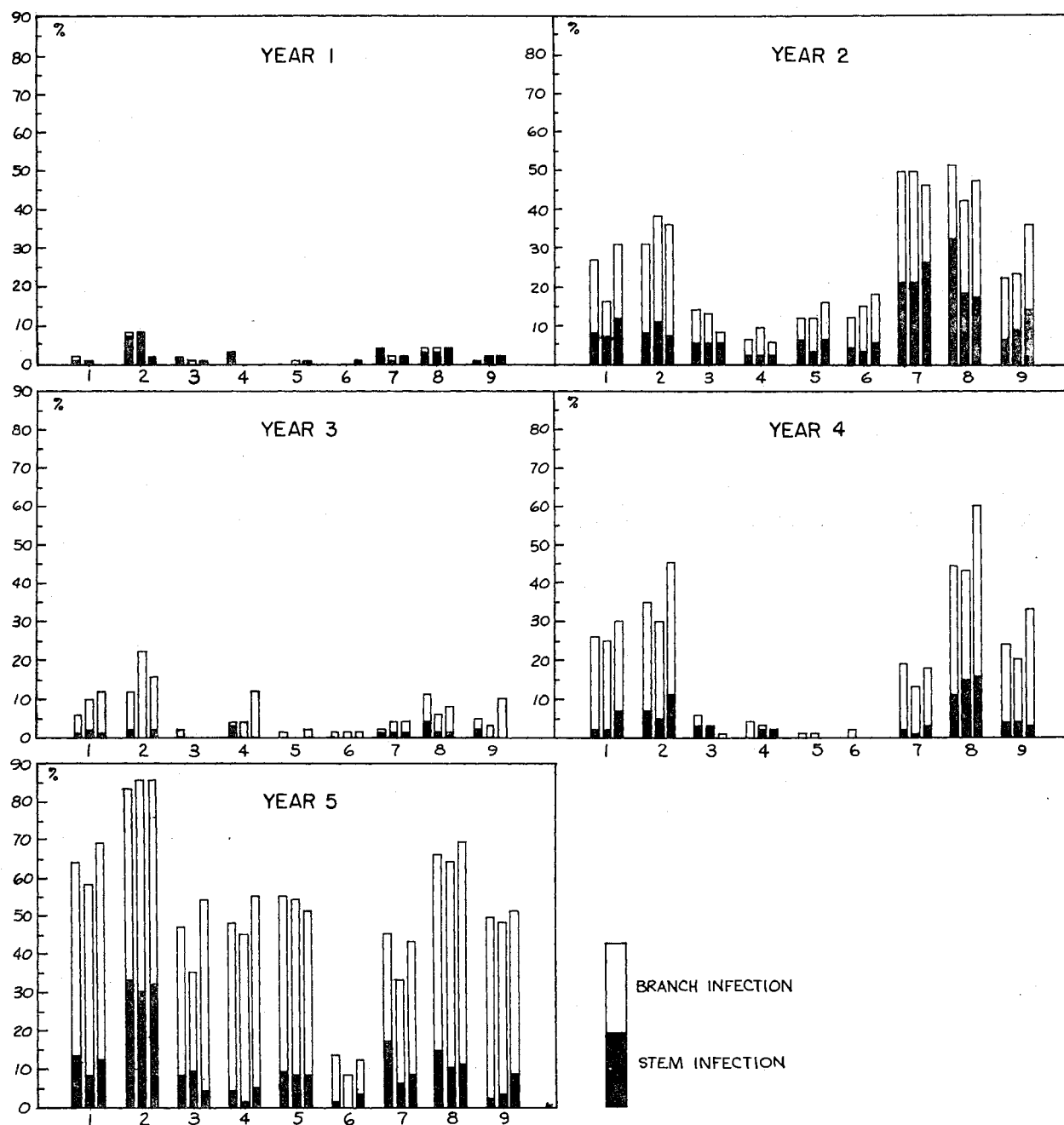


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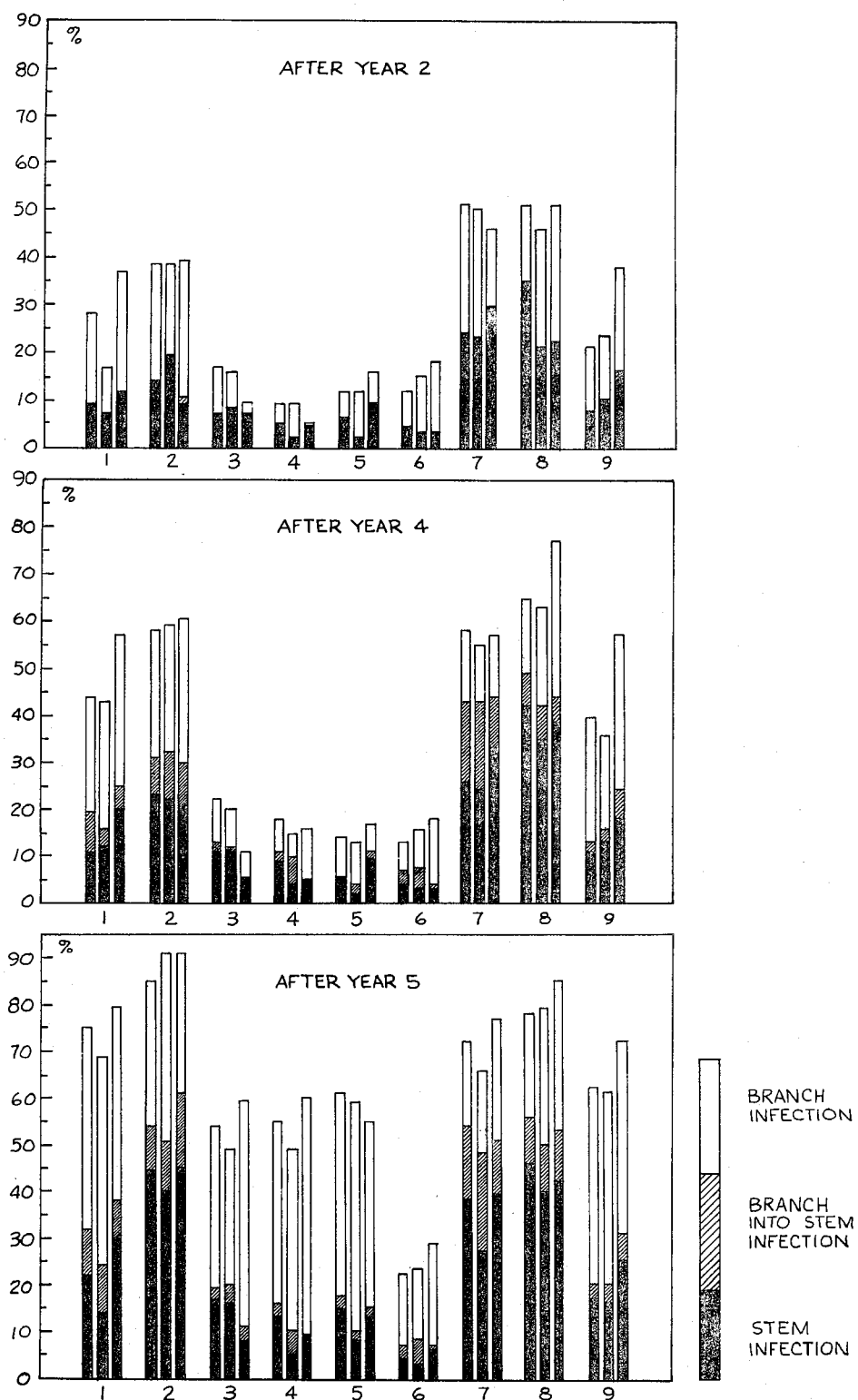


Fig. 3.--Percent cumulative infection in nine plantations after the second, fourth, and fifth growing seasons. The center bar is a seed source which was believed to possess some resistance to fusiform rust.

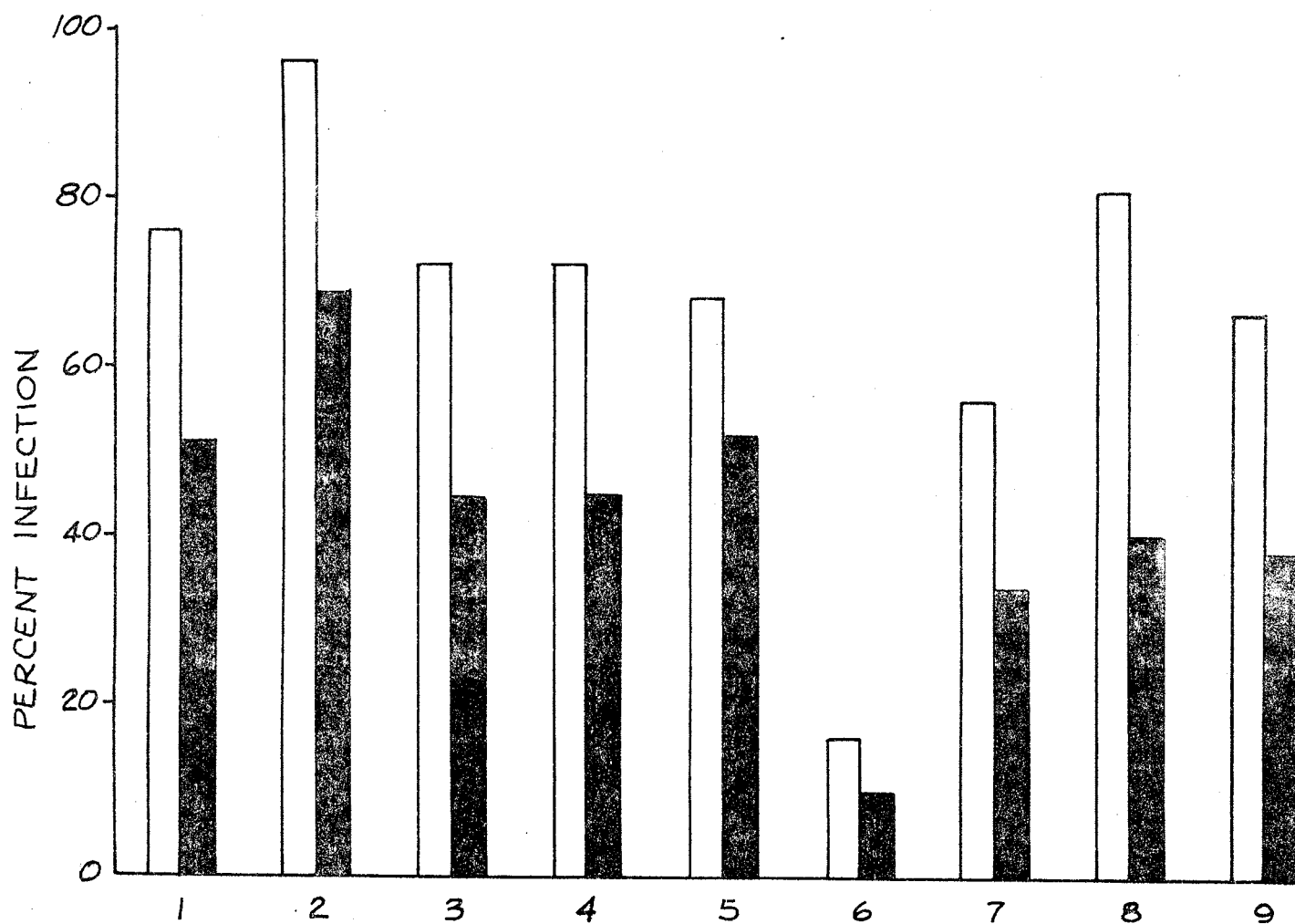


Fig. 4.--Percent of trees infected with fusiform rust in nine plantings in the fifth growing season. The bars on the left represent trees infected sometime prior to the fifth season, but the trees shown by the right bars were not infected before the fifth season.

THE CONCEPT OF ADAPTATION FOR CRONARTIUM QUERCUUM

G. A. Snow<sup>1/</sup>

Abstract.--Results of two cross inoculation experiments support the hypothesis that formation of round pine galls is an expression of resistance to Cronartium quercuum (Berk.) Miyabe ex Shirai. The evolutionary process of the pine oak rusts appears to have advanced further on pine species that are not severely damaged by these organisms than it has in loblolly and slash pine. Present resistance programs may be guiding the evolution of the loblolly pine-C. quercuum pathosystem in the same direction as exists with such pine species as shortleaf and Virginia.

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Red Creek is a small stream that intersects with Highway 49 about 35 miles north of Gulfport, Mississippi. This stream originates northwest of Wiggins, Mississippi, and enters the Pascagoula River, which flows into the Gulf of Mexico. The virgin forests in this area were cut during the late 1800's and most of the second growth timber has been cut again since that time. Many places near the river have not been converted to farms or pine plantations and the forest composition is probably similar to the original forest. Loblolly and shortleaf are the predominant pine species.

I first visited these forests a few miles west of Wiggins in 1964 with Frederick Jewell. He showed me galls of a pine-oak rust on the shortleaf pines that were round in contrast to the typical long fusiform galls on the adjacent loblolly pines.

We considered the possibility that the galls on both pine species were caused by the same fungus. Attempts to confirm this belief led to many different experiments at our Gulfport laboratory on variation in the pathogenicity of

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the Cronartium rust fungi. I will discuss two of these experiments with regard to how the results support the hypothesis that formation of round galls is an expression of resistance to C. quercuum. The results indicate that gall shape may be useful in assessing resistance and are the basis for speculation I want to make on the evolution of the pine-oak rusts.

In 1967, Al Kais and I inoculated five species of pine--sand, jack, short-leaf, loblolly, and slash--with inocula that was derived from the same pine species, with one exception (2). Inocula from sand pine was not available, and inocula from Virginia pine was used in its place (Fig. 1). Two single gall inocula from each source were used to inoculate 16 pine seedlings of each species. Disease readings were made 6 and 12 months after inoculation.

Our interpretation of results were that the differential response of the pine species demonstrated racial variation in inocula from Virginia, jack, and shortleaf pine. We pointed out that inocula from each pine species was most virulent on the same pine species, but was capable of infecting one or more other pine species. We also noted that inocula from Virginia, jack, and short-leaf pine usually caused round galls on all species, and that inocula from slash and loblolly pine caused spindle-shaped galls. An exception was that one of the inocula from Virginia pine caused both types of galls on sand and loblolly pine. This was in conflict with the common view of that time that the rust on loblolly and slash pine was a distinct species (C. fusiforme Cumm.) that caused only long galls and that round galls on all pine species were caused by C. quercuum.

Hal Burdsall was subsequently encouraged to study the taxonomic status of these rusts, and this included a re-evaluation of this experiment (1). He suggested that all the pine-oak rusts which cause galls on the stems and

branches of pines be classified as C. quercuum and those forms that are especially virulent on certain pine species be designated forma speciales. We speculated that the special forms likely have a common ancestor and that pathological differences are likely a result of adaptation to the different species of pines.

The most interesting thing I found when reviewing this study was the gradation in size of galls for combinations such as shortleaf inocula on loblolly seedlings. All the galls on these trees were round, but their size ranged from 1-2 cm. in diameter down to slightly raised spots on the stem. The latter would be considered by most researchers to be typical resistant reactions. Relative to the large fusiform galls for some other host-inocula combinations, I think all of these reactions--including the small round galls--can be considered as expressions of resistance.

In 1978 and 1979, Bayne Snyder, Warren Nance, Jim Hamaker, and I tested 43 loblolly pine families for resistance to C.q. f. sp. fusiforme (3). The pine families were from 10 control-pollinated pines in Livingston Parish, Louisiana. The trees had been intercrossed to make a half diallel with 45 possible crosses. Seed were available from all but two of the crosses. Trees from this experiment had been planted on the Harrison Experimental Forest in Mississippi in 1968.

Ten 5-week-old seedlings from each of the 43 pine families were inoculated with each of five different inocula in 1978 and the entire procedure was repeated a year later. The inocula were chosen to be diverse in virulence on the stock. Each inoculum was derived from one loblolly pine gall, the collection points for all inocula were widely separated, and two inocula were from Livingston Parish trees. Inoculum A was from a tree growing in Livingston Parish; inocula B, C, and D were collected near Jasper, Texas; Kiln, Mississippi; and Brewton, Alabama,

respectively. Inoculum E was from a tree in the diallel planting on the Harrison Experimental Forest.

Six months after inoculation, the seedlings were scored for presence of galls, gall lengths, and diameters. The variables selected for analyses were percentage of plants with galls and gall form (gall length/gall diameter). Gall form is a measure of shape; round galls produce values near 1, while long galls yield larger values.

Analyses with both variables revealed significant differences among both inocula and pine families, and significant family x inocula interactions. However, separation of inocula was more precise with gall form than percent galled. This was because there was less replication-to-replication variation in the gall form data than in the percentage data. The percentage levels were uniformly high for most family x inocula combinations.

More than 70 percent of the trees developed galls in 45 of the 50 half-sib family x inocula combinations (Fig. 2). Families 3, 5, and 7 had the lowest percentages and families 3 and 7 showed the most variation with inoculum source. Inoculum A ranked first or second highest on five of the six more variable families. The other inocula did not rank consistently either way.

The rankings of the five inocula were much more consistent with the gall form values (Fig. 3). Inoculum A ranked first or second highest on all half-sib families. Inoculum E also ranked high while inocula B and C ranked lowest on most families. Thus, galls caused by inocula B and C were rounder than those caused by A, E, and D.

Gall form was generally related to percent galled in that families 3, 5, and 7 with the lowest percentages (Fig. 2) also had the lowest gall form values (Fig. 3). Conversely, families 4 and 8, which ranked first and third for highest percentages had the largest gall form values.

I believe the relationship between gall form and percent galled in this experiment is further evidence that development of round galls is an expression of resistance. Whether the mechanism that limits longitudinal growth of the rust fungus is different from that which limits its establishment is unknown. It appears likely that we are seeing quantitative differences of the same mechanism.

It is interesting to consider gall shape in speculating on the evolution of the pine-oak rusts in North America. Perhaps the evolutionary process has progressed further in pine populations that are not severely damaged by these organisms than in those that are. Pathosystems such as the shortleaf-C. quercuum complex may be the result of co-adaptation of both host and pathogen. The fungus population in this system appears to be maintained at a moderate level and the predominantly round galls do not excessively damage the hosts. Shortleaf pines with long, damaging galls may have once been present but were eliminated from the population because of the poor fitness of the trees and inocula involved.

Our present resistance programs appear to be guiding the evolutionary process in loblolly pine in the same direction as shortleaf and Virginia pine. If the trees in the diallel experiment had been tested by current screening procedures, the parent trees for families 3, 5, and 7 would likely have been selected as the best candidates for rust resistance. Since these trees also tended to have small, round galls, continued use of such stock should result in a more innocuous pathosystem with loblolly pine than we now have.



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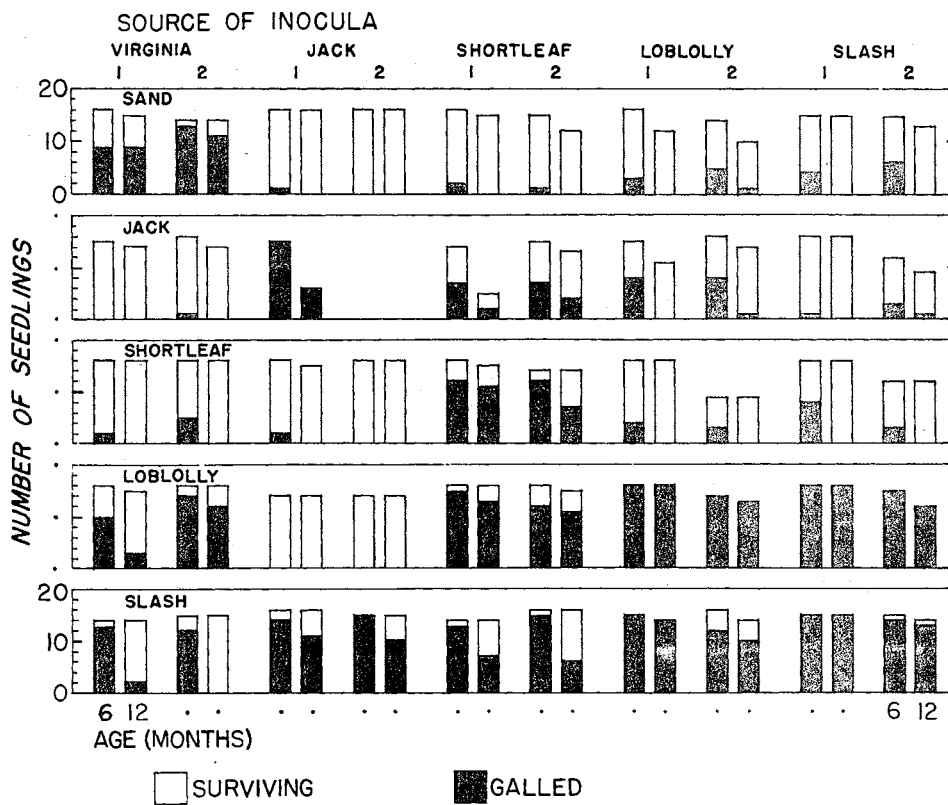


Fig. 1.--Gall development on five species of pine inoculated with five sources of *Cronartium quercuum*. From data of Kais and Snow (2).

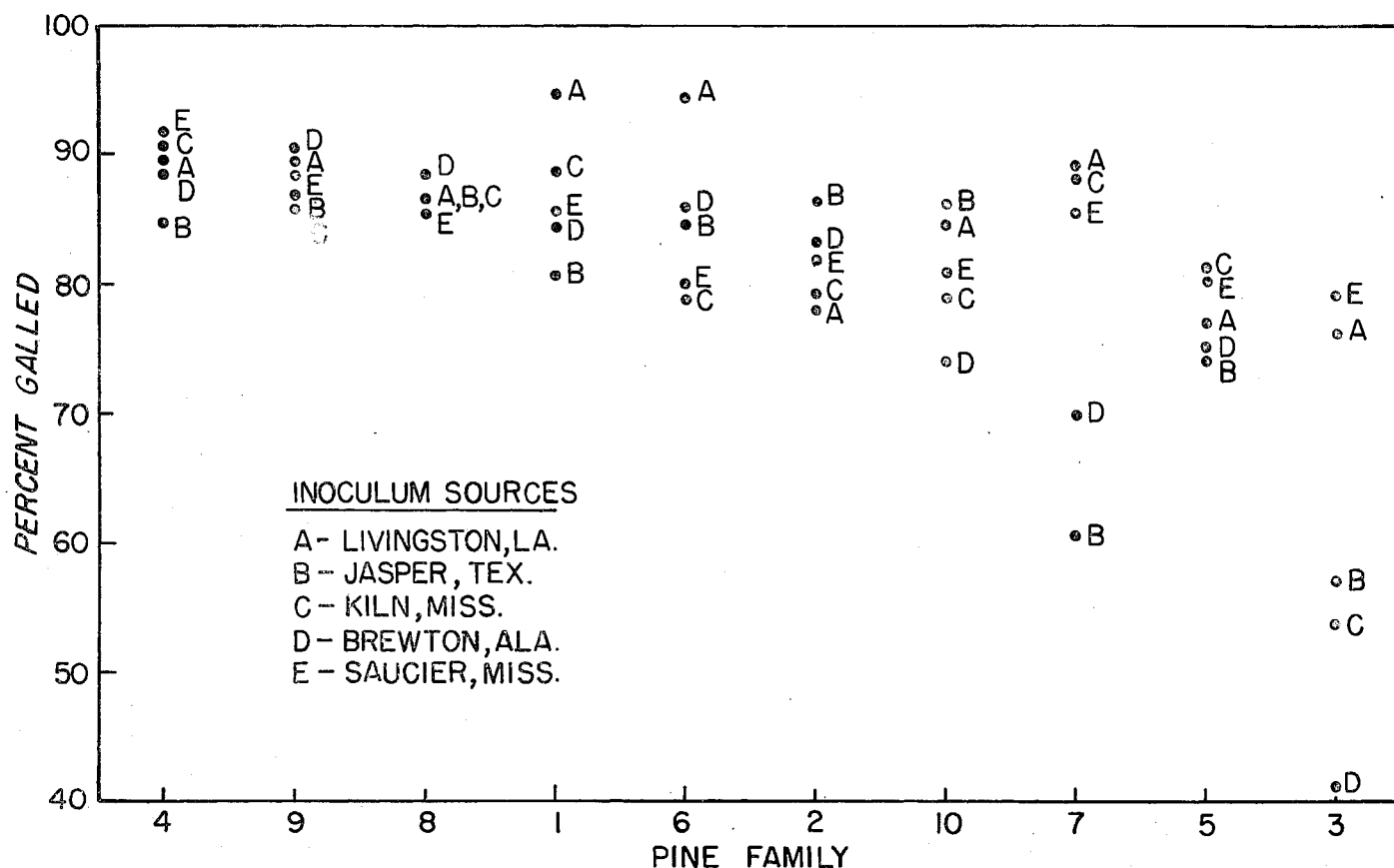


Fig. 2.--Percentage of trees with galls for 10 half-sib families of loblolly pine after exposure to five sources of inocula from loblolly pine. The half-sib family values are an average of eight or nine full-sib families with a common parent; family numbers correspond with the common parent numbers. Families are ranked in decreasing order of susceptibility. From Snow et al. (3).

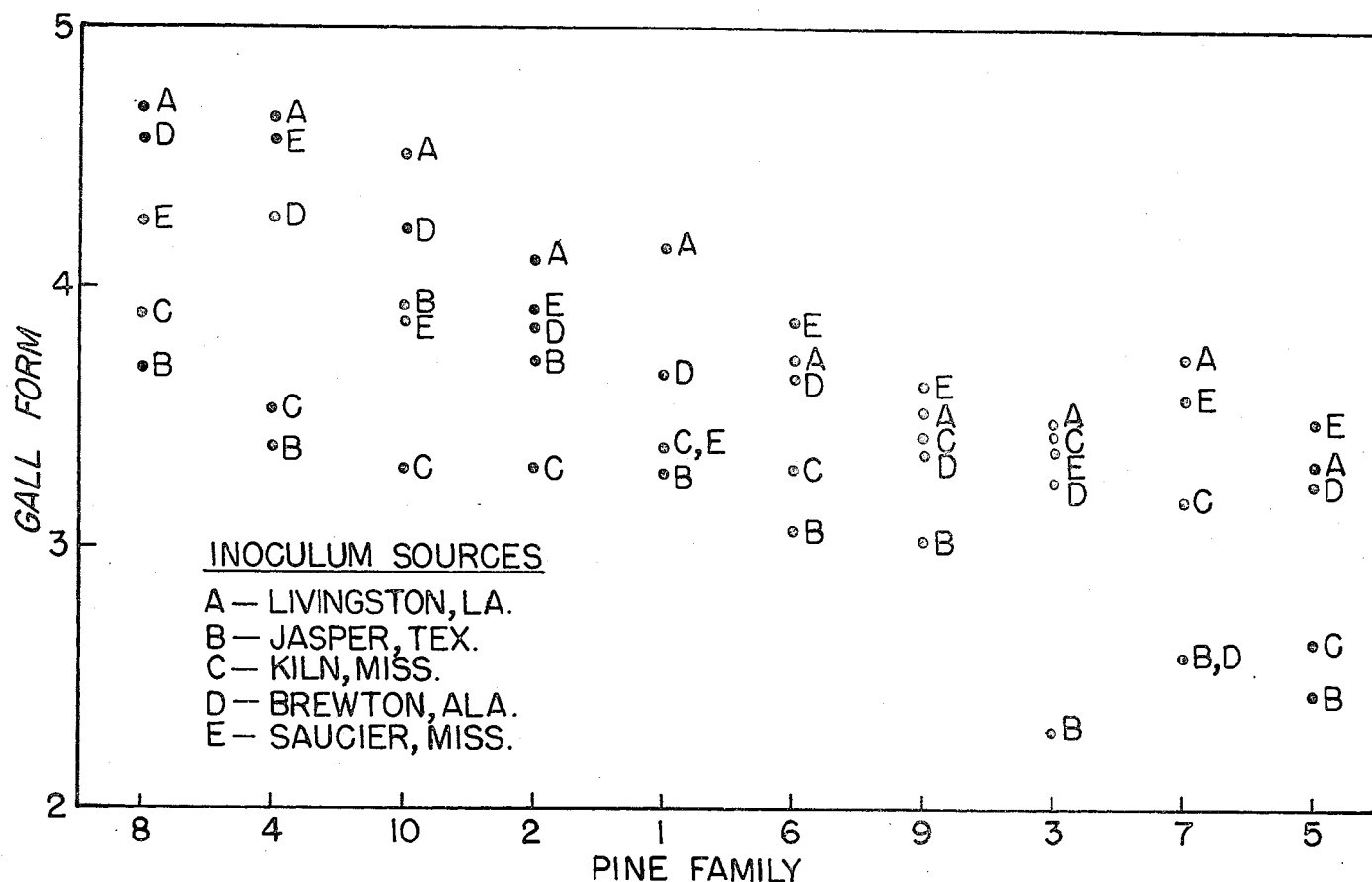


Fig. 3.--Form (gall length/gall diameter) of galls on 10 half-sib families of loblolly pine after inoculation with five sources of inocula from loblolly pine. The half-sib family values are an average of eight or nine full-sib families with a common parent; family numbers correspond with the common parent numbers. Families are ranked in decreasing order for average gall form values. Each entry represents the mean gall form for all galled trees in a particular family x inocula combination. From Snow et al. (3).

Impact of Native Insects on  
Off-Site and Marginal Plantations

by

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The impact of native insects on off-site and marginal plantations is a very broad topic so it has been limited to make it more manageable. Several examples will be given suggesting that off-site seedlings have been damaged by native insects which ordinarily do not cause this type of damage. In these examples, the definition of an off-site plantation includes plantations established from seed from an unknown source or a source from outside the appropriate seed zone, located at the periphery of the type, on sites with extreme competition or on sites with insufficient or unbalanced soil nutrients. After these examples, some principles will be pointed out which should be considered when culturing genetically superior stock.

What is to be described is not "scientific" in the sense that the information is replicated, statistically sound, and published in a refereed journal. The information consists of observations by field entomologists and foresters. They have made recommendations to land managers based upon the "state of the art." At first, the observed phenomena were not thought to be native insect damage to off-site plantations. After discussions and further evaluation, it was concluded that native insects appear to be attacking off-site plantations. The information has survived as anecdote.

The first example was found on the Rogue River and Winema National Forests in southern Oregon. There are several old burn areas where pine previously occupied the site. The rehabilitated areas were planted with pine seedlings from seed of unknown origin. The planted stand survived just long enough to become a nurse crop for natural regeneration of the areas. When the plantation reached 12 to 15 feet in height, most of these trees were attacked by *Ips pini*, pine engravers. The natural ponderosa pine seedlings were not affected and remain free of pine engravers. Pine engravers are normally found at non-damaging levels. Large numbers will develop in host material such as freshly cut logs, slash over 2 inches in diameter, windfall and tops and limbs of trees killed by *Dendroctonus* beetles. The plantation, not meeting any of these conditions, must have been susceptible for other reasons. The conclusion drawn was that the original planted seedlings were off-site, therefore under stress, and so particularly susceptible to attack by or attractive to pine engravers found in the area.

The second example occurred in 1969 on the Bly Ranger District, Fremont National Forest. *Pissodes schwarzi*, the Yosemite root weevil, was found girdling and killing the residuals in a recently thinned plantation of Jeffrey pine. This weevil is known to mine the thick bark of normal, injured, dying, dead and felled trees and stumps, and also the bases and stems of young saplings of sugar, white and yellow pines. This example was the first report of the Yosemite root weevil damaging residuals in a thinned Jeffrey pine plantation in Oregon. Nearby in California the weevil was found causing damage to off-site plantations of Jeffrey pine. What is seen in this instance is a normally innocuous weevil becoming severely damaging. It is suspected that this is due to the trees being off-site or the attributes of the site weakening or suppressing the trees. Insects are renowned for being opportunists. In this case, they increased their populations in the slash and then sought out other suitable, perhaps stressed, host material.

A recent situation which has not been evaluated by an entomologist but which is interesting and deserves some attention is a ponderosa pine plantation on the BLM's Lakeview District. This is a young plantation, less than 2 years old, planted on the desert fringe with stock that is from its seed zone. This can be considered an off-site plantation by the definition being used as it is a site at the periphery of the forest type. Approximately 70 to 80 percent of the seedlings had their terminal bud destroyed. The damaging species has not been collected and identified. The insect which is most likely to have caused the damage described is the ponderosa pine tip moth, *Rhyacionia zozana*. This species, while generally not seriously destructive, will damage open-grown seedlings and saplings less than 2 meters tall. Although it has not been recorded as attacking off-site plantations, closely related species such as the southwestern pine tip moth, *R. neomexicana*, are known to damage seedlings on poor sites.

From these three examples, even though anecdotal in nature, we may intuitively conclude that there are conditions or circumstances where damage can be expected from native insects that normally exist at nondamaging levels. Information from a variety of sources about insects responding to stressed plants suggests principles to consider in our forest tree improvement programs. Reference will be made to examples where moisture availability and site competition affect populations of insects.

The relationship between secondary plant substances and phytophagous insects was described by Fraenkel (1959). His original ideas were updated (Fraenkel 1969) to include functions for these substances in physiology and development.

Entomologists generally accept that the qualitative nutritional requirements of phytophagous insects are very similar. What differs and what is important is that their relative (quantitative) nutritional balance varies (Dadd 1973).

Beck and Reese (1975) and Chapman (1974) are recent reviews of metabolic aspects of insect-plant interactions and chemical inhibition of phytophagous insect feeding, respectively.

Ovarian quality differences may be related to nutrition in gypsy moth (Leonard 1970) and western tent caterpillar (Wellington and Maelzer 1976). Capinara et al (1977) implicated yolk quality and quantity to influence gypsy moth population quality.

From these references, the principle that has meaning in forest tree improvement programs is that native insects will respond to trees in a stressed state. The response will usually be an increase in populations and damage to the plantation.

White (1974) offers a hypothesis to explain outbreaks of a looper in Monterey pine plantations in New Zealand which were found to be under moisture stress.

For most of the time, most of the young produced in a population of phytophagous insects die from a relative shortage of nitrogenous food. The essential nitrogenous nutrients in the food plants are too dilute in relation to the amount of nonnutritious material that the young insects must "process" in order to provide protein for their very rapid growth. Occasionally their food plants become a rich source of nitrogen when stressed by random fluctuations of the weather, and the result is that many more young insects survive.

When plants are physiologically stressed, there is an increase of nitrogen, and especially of the amino acids transported in the phloem. Part or all of a plant may be stressed by anything which limits the supply of water to its tissues. Two environmental factors simultaneously affect many plants over a large area are drought in the summer and excessive soil water in winter, resulting in waterlogging and suffocation of feeding roots.

Should a combination of wet winters and dry summers persist for several consecutive years, phytophagous insects could greatly increase in abundance due to their high reproductive potential.

White's hypothesis was developed from work on several insects, but the relation between site, climatic fluctuations and insect outbreaks was developed from loopers on Monterey pine plantations. Monterey pine is an introduced species to New Zealand. The species may not be fully adapted to the extremes of site or climate in New Zealand. The plantations were on areas of hardpan, so there were areas where there was stress on the plants from the breaking of feeding roots, suffocation of roots in the winter because of flooding and lack of water in the summer due to poor storage capacity of the soils and high evaporation potential. The loopers increased their populations in these hardpan areas and then moved to the remaining plantation.

Another type of insect response is to trees that are in competition for the various attributes of their site. In the next example, insects responded to trees under stress by changes in their behavior. Within the discipline of chemical ecology, the use of secondary metabolites to affect population biology or behavior is termed allelochemicals (Whittaker 1970).

Waring and Pitman (1980) have proposed a model of host resistance to bark beetles. They hypothesize that the amount of carbohydrate reserves available controls host resistance. Also, the monoterpene chemistry of the phloem which affects beetle behavior differs when reserves are high or low.

This model is based upon the fact that trees must satisfy certain requirements before they produce stemwood. Trees supply nutrients to roots, shoots, and cones before producing stemwood. A decline in stemwood production would indicate that their carbohydrate reserves were limited. Because of these low carbohydrate reserves, Waring and Pitman (unpublished data) suggest that the trees lack the ability to produce sufficient quantities of defensive compounds. One might also infer that the trees are more "attractive" to the beetle because of changes in phloem monoterpene chemistry.

Larsson et al (1982) and Mitchell et al (1982) have shown that the damage susceptibility of ponderosa pine and lodgepole pine from mountain pine beetle is closely related to tree vigor. Tree vigor can be increased by stocking control. Vigorous trees are probably less attractive to the beetles and are more apt to repel attack. Below a vigor threshold, mountain pine beetle attacks are likely to be fatal.

Berryman (1982) reconciles contradictory explanations for mountain pine beetle outbreaks in lodgepole pine forests. He concludes that silviculture aimed at maintaining tree vigor seems to offer the most promise for preventing outbreaks.

The two examples described here provide additional support for opinions that many foresters and entomologists developed intuitively from observation. Generally, trees under stress are more susceptible to successful insect attack and damage or mortality. This generalization has application and should be kept in mind when planning forest management or tree improvement activities. Silvicultural prescriptions should include measures to reduce the potential impacts of insects. While we do not have specific, replicated, and recorded information on the impact of insects on various forest tree plantations, we do have the opportunity to design the evaluations of plantations to gain this information. In addition to care in establishing plantations with expensive, genetically improved stock, it is incumbent upon the forester to have planned actions to maintain a vigorous forest through its rotation to minimize the impacts of insects and diseases. The tree improvement specialist has a responsibility in seeing that the stock is grown in a manner which exploits the tree characteristics selected for their program.



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Impact of Native Diseases in  
Pacific Northwest Off-Site Plantations

Ry

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Dictionaries do not list "off-site" as a word. A more appropriate term would be misplaced plantations. However, since the illegitimate word off-site is in every forester's vocabulary, I will continue to use it. It is understandable why off-site is not a word because it is extremely difficult to define and probably impossible to quantify. Off-siteness, off-sitedness or misplacement is all relative. When is a plantation off-site? When the regeneration material was collected 500 feet lower in elevation on the same mountain than it is planted on? When the seed source is 10,000 miles away from the planting site? The answer is yes, no, and maybe in both situations.

Modern day professional foresters understand the importance of making certain forest regeneration materials are well adapted to the sites on which they will be established. In general, native species already thriving within the immediate reforestation area will perform better than species imported from distant locations. If nonlocal regeneration materials are to be used for plantation establishment, the climate and soils of the plantation sites should closely match those of the original collection sites. Climatic criteria are: (1) mean and extreme temperatures; (2) length of growing season; (3) amount and timing of precipitation; and (4) latitude.

Plantations can be misplaced in at least three different ways. Disease implications vary somewhat with each. I will use examples from the Pacific Northwest to illustrate each.

The most obvious way off-site plantations are established is movement of a tree species out of its native range into an area where it does not occur. We are probably all familiar with famous horror stories such as the severe *Dothistroma* needle blight outbreaks on Monterey pines moved from California to New Zealand and debilitating Swiss needlecast on Pacific Northwest Douglas-firs also grown in New Zealand. This long-distance movement of regeneration material no longer takes place on National Forests in Oregon and Washington, but it did several years ago.

Regeneration materials are sometimes moved out of their native ranges, but usually the distances involved are just a matter of a few miles. In some cases, movement of only a few hundred yards will take a tree species out of its native range. Diseases of abiotic origin are the major problems in the Pacific Northwest when tree species are regenerated on sites higher or lower

in elevation than where they occur naturally. Douglas-firs planted at high elevations in the Cascades above where the species occurs naturally often suffer severe breakage and deformities from snow. Frost damage is also common on Douglas-firs planted above their normal range. True firs, such as Pacific silver fir and noble fir, that normally grow at high elevation suffer from heat damage and foliage dessication when planted at lower elevations. Diseases caused by fungi are usually not important when regeneration materials are moved out of their natural ranges in the Pacific Northwest. The reason why diseases of biotic causes do not cause large impacts in these plantations are most of the parasitic organisms are host specific and have many of the same ecological requirements as their hosts. Parasite and host ranges tend to be nearly identical.

A second way plantations are misplaced is movement of regeneration materials many miles away from their points of origin to other locations within the natural ranges of the species. Diseases of both abiotic and biotic causes adversely impact these plantations. Frost and foliage dessication are the most common abiotic problems that occur when seed sources are moved to locations higher or lower than their points of origin. Diseases caused by biotic agents such as fungi are more serious in these plantations than those established outside the natural range of the tree species. The parasites that cause the diseases are probably already in place, but the local seed sources over hundreds or thousands of years have probably reached some form of balance with them.

Eastside Douglas-fir seed sources planted in westside sites are much more prone to infection and defoliation by *Rhabdocline* needlecast than westside seed sources established on the westside. Root rot caused by *Armillaria mellea* is a common problem in Douglas-fir plantations established from nonlocal seed sources. *Armillaria* root rot occurs in many Douglas-fir plantations established with local seed sources, but total mortality seldom exceeds two or three percent and stops when plantations reach an age around 25. In off-site Douglas-fir plantations, *Armillaria* mortality may exceed ten percent of the stocking and continue throughout the life of the stand. In many of these plantations, *Armillaria*-caused mortality will not begin until the stands are at least 10 years old.

A third way in which plantations can be misplaced is to make relatively large pure or nearly pure plantings in areas where the tree species does occur naturally but as a minor component of the stand. Some would argue such plantations are not off-site since the seeds are collected on the same areas the seedlings will be planted in. I suggest they are off-site since under natural conditions, pure stands of the species never occurred on the sites. These plantations are usually not seriously troubled with abiotic diseases because the local seed sources have had hundreds or thousands of years to adapt to the local climate. Diseases of biotic origin can cause serious problems because the parasites of the species are probably already present. Ponderosa pine does occur naturally, but as a very minor component of stands on the westside of the Cascades in southern Oregon. Pure plantations of ponderosa pine established in the 1950's performed reasonably well until the late 1960's when a needlecast outbreak caused by the fungus *Lophodermella morbida* caused severe decline and tree killing in the plantations. Virtually all trees in infected plantations were infected. The few remaining plantations are still infected. Contrary to some foresters' opinions, local seed sources are not resistant to the fungus. The abnormal concentration of suitable host material enabled a native fungus to increase its inoculum load many thousand times greater than experienced before the plantations were established. Prior to the time large plantations of

pine were planted, the inoculum load was probably so small that the scattered pines in the stand escaped infection or were only lightly infected. A similar example but with another disease is occurring in Douglas-fir plantations on the Olympic Peninsula in Washington. Douglas-fir was a minor component in natural stands comprised mainly of western hemlock, Pacific silver fir, and western redcedar. The stands were clearcut and planted with Douglas-fir from local seed sources. Armillaria root rot began killing large numbers of Douglas-fir when the plantations reached about 5 years of age. Naturally regenerated western hemlock and Pacific silver fir are not affected.

Losses from several diseases can be prevented by using local regeneration materials for plantation establishment. Some movement of regeneration materials is inevitable and, in some instances, the results will be better than if local seed sources are used. Performance of seed sources should be monitored in evaluation plantations. In the particular case of diseases, trees may perform well for 10 years or more before diseases appear and begin to cause serious losses. Disease evaluation has to be an important aspect of evaluation plantation monitoring.

Genetic Gains Realizable in Rust Resistance  
Programs--What Are We Buying? 1/

by

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June, 1982

- 
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## Introduction

Jerry Franc, in an earlier paper in this workshop, described the breeding program generating the western white pine orchard seed we use in our operational reforestation program. The present paper focuses on describing the benefits of using this blister rust resistant seed in operational reforestation in the Northern Region. This description assuredly will not exhaust the topic "Genetic Gains Realizable in Rust Resistance Programs," but will exemplify how resistant material perhaps ought to be viewed. The view is from the perspective of folks who have been planting resistant white pine for nearly a decade now.

In a later section, we compare alternative management regimes for two stands on the Wallace Ranger District of the Idaho Panhandle National Forests. In these comparisons, we exemplify benefits of predictable stocking control and species diversity discussed in other sections, considering no white pine, susceptible white pine and moderately resistant white pine alternatives.

### Resistance Levels

Nine sources of white pine seed ranging from 25 percent to 60 percent resistant are approved for planting in the Northern Region (Table 1), but, to date, virtually all resistant white pine stock emanated from three seed orchards (Sources 1, 2 & 3 in Table 1). This paper describes the benefits of using this orchard seed. The principal purpose for developing sources displaying lower levels of resistance is to permit the matching of resistance level to site hazard (for rust infection). (We are working now with IFRES to implement a hazard rating scheme for planting sites.)

The resistance level of two of the seed orchard sources described in this paper is 60 percent, and the third is 35 percent (Table 1). By this we mean that 60 percent or 35 percent, respectively, of the white pine trees planted will be able to survive blister rust and grow normally to rotation age, under the most severe infection conditions, conditions in which about 10 percent of native wild trees would survive (this is the survival level we call "susceptible" in this paper). Some surviving resistant trees will be infected and display symptoms.

### Demand vs. Supply

The Regional Forester banned the planting of western white pine in operational reforestation in the Northern Region from 1964 through 1973. Managers of white pine had concluded that susceptible white pine in plantations would create more problems than it was worth, principally in stocking control (more on this later).

In 1974, the first operational rust-resistant white pine stock in the Region's history was planted on the Palouse Ranger District of the Clearwater National Forest. The plantation was dedicated to Dick Bingham.

TABLE 1

## Approved Sources of Operational

## Western White Pine Seed

	Name of Orchard, Plantation or Stand	Estimated Resistance (%)*	Location		Collected by
			Forest	District	
1.	Cd'A Nursery Orchard	60	IPNF's	Nursery	Nursery
2.	Sandpoint Orchard	35	IPNF's	Sandpoint	Sandpoint RD
3.	Moscow Arboretum	60	IFRES	-	R-1 Selective Breeding Specialist (SBS)
4.	Canyon Creek Test Plantation	40	IPNF's	PREF	IPNF's (or R-1 SBS)
5.	Merry Creek Test Plantation	40	IPNF's	St. Maries	IPNF's (or R-1 SBS)
6.	Elk River Test Plantation	28	CLW	Palouse	CLW (or R-1 SBS)
7.	Fernwood Test Plantation	28	IPNF's	St. Maries	IPNF's (or R-1 SBS)
8.	Natural Selection SPA	25	Specify	Specify	Forest (or R-1 SBS)
9.	Phase 2 Plus Trees	25	Specify	Specify	Forest (or R-1 SBS)

\* Genetics Project Leader, IFRES Moscow, will provide research publications, on request, confirming these estimates.



In nine years, now, 3,249,340 seedlings have been planted in operational reforestation projects on six National Forests. For 1974 and 1975, the supply of seed (Table 2) exceeded the demand, primarily because "the word wasn't out yet." Then, until 1981 when the bank was inflated by a bumper 1980 seed crop, the demand exceeded the supply, in some years enormously. Clearly, silviculturists on white pine Forests were convinced white pine was beneficial, even though not immune and sometimes only 35 percent resistant.

## White Pine Management

### The Desirability of Western White Pine

Western white pine is favored over alternative species for the same site for several reasons. The first are its faster growth rate and higher stumpage value (more on this later). White pine is less damaged by insects and diseases (except for blister rust) than are other species, and it often proves surprisingly free of animal damage--e.g. browsing or rodents--when other species in the stand are devastated. White pine is more plantable than other species, and because of lower planting shock white pine "takes off" quicker and suffers less mortality.

On south and southeast facing slopes the availability of white pine planting stock offers the opportunity for a three-species mix in stands which would have been stocked with only two species (e.g. DF and PP) during the 10 years of the white pine planting moratorium. In a worst-case scenario--total destruction of one species from insects or disease during the rotation--the stand could more nearly maintain full stocking if one of three rather than one of two species were lost.

Moreover, for many insects (e.g. bark beetles) and some diseases, (e.g. dwarf mistletoe or root rots) proximity of host trees influences the severity of the damage. The more widely spaced the trees--as in a 3-species stand vs. a 2-species stand--the less severe the total damage from the pest.

Because white pine grows faster in its early years than other species on the site, sites planted with white pine recover visually and hydrologically faster than they would if alternative species are chosen. This rapid early growth is also important for capturing highly productive sites from competing vegetation, e.g. Ceanothus, willow, maple or menziesia.

### Objectives, Opportunities and Constraints

The typical white pine site managed for timber is highly productive--frequently exceeding 120 cu. ft/A/yr. and virtually always exceeding 80 cu. ft/A/yr. Ergo, timber optimization is often the goal.

Because of the moderate environment of the typical white pine site and the successional status of the species favored for this site, clear-cutting and planting is most frequently the regeneration system chosen.

TABLE 2

## WHITE PINE SEED ADDED TO INVENTORY

<u>Year</u>	<u>Quantity Added (Lbs.)</u>
1974	42.75
1975	90.25
1976	58.75
1977	38.25
1978	57.20
1979	433.20
1980	1.70
1981	564.00
1982	149.20
TOTAL	1435.30

Indeed, sites needing shelterwood treatment will be too dry for western white pine, even if it were planted under the shelterwood.

Another goal for these stands is a mixture of species. At least two species,--and on north-facing sites, three or more species are desirable. Were white pine planting stock not available, many clearcut sites might end up with only one commercially desirable species. Based on the composition of natural stands, the need for species diversity, and economics, the manager wants at least 25 percent (by volume) white pine in the stand at the end of the 80- to 110-year rotation. This goal ought to be reasonably achievable by planting 300 white pine trees per acre plus one or two other species, followed by a precommercial thinning at about 25 or 30 years of age and a commercial thinning at age 50 to 60 years. The schedule of planting and thinnings should create a stand neither severely over- or under-stocked.

On north-facing sites, this treatment sequence was unable reliably to create the target stand when only susceptible white pine was available. North-facing sites often were either severely overstocked at an intermediate entry or nearly devoid of a white pine component at rotation, depending on the vagaries of blister rust disease development. The overstocking problem could easily have been compounded by planting white pine on sites later occupied by several hundred or several thousand more volunteers of white pine and/or other species.

On south-facing sites, even knowing the site would seed in naturally, the silviculturist often chose to prescribe planting anyway, to ensure a white pine component at the end of the rotation. If severe infection were to kill 90 percent of the white pines in the stand, and if the manager wanted 25 white pine trees per acre at rotation, then the stand had to start with at least 250 trees per acre. Natural seeding couldn't always be counted on to provide 250 trees per acre.

Indeed, on south and southeast-facing clearcuts, white pine could rarely be expected to seed in sufficiently to offer a manageable component. Only planting could ensure that component, and if it were susceptible stock, the white pine stocking--again--would be determined more by the whims of blister rust disease development than by a predetermined schedule of stocking control treatments. But understocking--at least in the white pine component--was far more likely than overstocking.

The reliability of creating the target stand, with an affordable treatment sequence, was so low that planting white pine was abandoned for a decade. It was as unreliable for north-facing sites as for south-facing, but for different reasons.

#### Benefits

The faster growth rate of white pine persists through the rotation, so yields are increased if white pine is a significant component of the stand. Receipts are also inflated from the higher stumpage value of white pine.

Stumpage value differences between white pine and other species have historically been enormous. While many have predicted for 10 years or

more that gap would narrow, it hasn't yet. White pine (and ponderosa pine) is typically selling for about \$160/MBF while Douglas-fir rarely exceeds \$70 in current sales on the Wallace Ranger District. Other species are lower yet. Stumpage revenue from harvesting stands devoid of white pine (because of blister rust) clearly is reduced, compared to comparable stands with a white pine component. The trend is likely to continue.

Perhaps the greatest benefits for using rust resistant white pine are in reliable stocking control and reduced mortality rates. Here's how those factors reduce stand management costs.

On south-facing sites, if the silviculturist were to plant susceptible white pine, he might prescribe 1,000 WP trees per acre to ensure adequate stocking of white pine after blister rust takes its toll throughout the rotation. (On north-facing sites he wouldn't prescribe planting susceptible white pine, because he'd get all the naturals of that resistance level he'd want.) With resistant stock he may prescribe only 400 white pine trees per acre, so he has reduced his stock costs and variable planting costs by 60 percent (for the WP component of the planting mix). Benefit/cost ratios can be influenced.

Higher initial densities of white pine usually may result in higher precommercial thinning costs as well. Blister rust infection may be too poorly developed by precommercial thinning age to have killed many trees, so they have to be thinned to avoid overstocking. If the site is planted at lower densities and blister rust infection develops strongly, the stand will end up with an insignificant WP component and perhaps understocking.

The higher the susceptibility of white pine, the less likely is any one thinning to maintain its stocking goal. The phenomenon extends to all thinnings in the rotation. With susceptible white pine, the fewer the thinnings the less likely is the stand to achieve its stocking goals. Thinnings later in the rotation, however, will be less affected than early thinnings, because infected large trees are less likely to perish than infected young trees, and have fewer years to survive to the end of the rotation.

The economic consequence of overstocking or understocking is reduced yield. If the white pine component of the stand is 60 (or 35) percent resistant, rather than 8 percent or 10 percent, then stocking controlled at a given level of predictability may be achieved with fewer thinnings. Or, if we can afford only two thinnings in the rotation, we are more likely to attain projected stocking if the white pine component is 60 (or 35) percent resistant than if it is 8 percent or 10 percent.

#### Costs

To portray the added costs of using rust resistant white pine, we scrutinized seed, seedling and stand management operations.

### Seed and Seedling Costs

All the added costs for producing seed orchard seed are reflected in the price of orchard seed in the WCF inventory, versus nursery-run seed. Orchard seed is carried at \$485/lb. vs. \$75/lb. for nursery-run seed of white pine and other species.

Forests, however, don't care about white pine seed costs, because Forests never buy white pine seed, only seedlings. Bareroot seedlings of all species are priced the same--\$119 per thousand. Container seedlings are all \$163 per thousand (in Pine Cells). The white pine program, then, is subsidized by the programs in other species.

Most white pine, however, is grown in containers, while the majority of stock in other species is grown bareroot. A Forest choosing to plant white pine therefore may be incurring an added cost of \$44 per thousand, which is a 35 percent increase, but this is not a consistent added cost on Wallace.

### Cultural Treatment Costs.

We looked at possible differences in costs of tending (on the same site) stands with rust resistant versus susceptible versus no white pine. Differences, if they exist will be so trivial as to influence economic analyses very little.

### Economic Comparison of Alternatives

To illustrate the benefits of using rust resistant white pine in the Northern Region, we identified two sites on the Wallace Ranger District harvested and planted within the last six years. Three alternative prescriptions were written for the south-facing site, and three for the north-facing site. Each carried the stand through to rotation. Costs and benefits were compared. The alternative chosen for implementation for each site illustrates the benefits discussed in preceding sections of this paper.

#### The South-facing Site

This 25-acre site lies in the Ulm Creek drainage on the Wallace Ranger District on a southeast-facing slope of about 60 percent. Its productivity is about 100 cubic feet per acre per year (MAI). The Habitat Type is grand fir/Pachistima. The elevation is 4200'. The soil is angular, gravelly subsoil over highly fractured metamorphic bedrock and overlain with a loess cap of variable depth.

The site was clearcut and regenerated in 1978. We compare and contrast the existing stand with two other alternatives which realistically might have been chosen. Each alternative is projected to rotation, using the IFRES Prognosis Model. Economic comparisons employed the model CHEAPO (Computerized Help for the Economic Analysis of Prognosis-model Outputs), which is tied to the Prognosis Model. Assumptions common to all three alternatives were:

. The stand is commercially thinned to 100 trees/A at age 64 years.

. The stand is clearcut harvested and regenerated 100 years from now (culmination of MAI).

. The cost of site preparation and planting are considered sunk costs.

. The real value of stumpage increases at the rate of 2 percent per year over the next 100 years.

. Discount rate = 4 percent.

. Specifications on three tree product categories; large sawtimber, small sawtimber, and poles. By specifying a difference in size classes, value revenues could be determined for each species by tree size.

. Minimum removal volume of 2.5 MBF/acre to be considered a commercial operation (57).

. Specified stumpage revenue values by tree product category and species. These stumpage values were obtained using the Idaho Panhandle National Forest's Stumpage Valuation Equation. This equation was developed by regression analysis using data from 65 major timber sales sold on the Idaho Panhandle National Forests.

Alternative 1--plant 60 percent resistant white pine, Douglas-fir, and ponderosa pine. This is the existing stand. About 300 trees per acre of white pine (60 percent resistant), ponderosa pine and Douglas-fir were planted. Volunteers, mostly of grand fir, have brought the stocking up to 480 trees/A today, 40 percent Douglas-fir, 25 percent grand fir, 19 percent white pine and 13 percent ponderosa pine. The Prognosis Model shows no need for a precommercial thinning because natural mortality is expected to reduce stocking to about optimum level until age 64 years. Our experience, however, suggests we can expect enough ingrowth on these sites that a light precommercial thinning will be necessary at about 34 years. The Prognosis Model does not account for such ingrowth.

The stand is to be commercially thinned, favoring the white pine more strongly than Douglas-fir and ponderosa pine. As a consequence of this thinning and low mortality in white pine (appendix 2), the proportion of white pine will be increased to 30 percent of the trees per acre at rotation. About 31 percent of the regeneration harvest volume will be in white pine.

The total volume harvested in the regeneration harvest will be 53,422 BF/A. An additional 5,808 BF/A will have been harvested in the commercial thinning, bringing the total volume to 59,230 BF/A.

Discounted total revenues are \$410.45. Discounted total costs are \$83.69. The net present value is \$326.76, and the benefit/cost ratio is 4.90.

Alternative 2--plant Douglas-fir and ponderosa pine. In this alternative only Douglas-fir and ponderosa pine would have been planted, 361 trees per acre. Some natural white pine (10 percent resistant) and grand fir volunteers would have brought stocking to 510 trees per acre today, 59 percent Douglas-fir, 18 percent grand fir, 12 percent white pine and 12 percent ponderosa pine. Here, again, the stand would be precommercially thinned at age 34 years.

The mortality rate of white pine would be so high and initial stocking so low that the proportion of white pine would be only 3 percent of the trees per acre at rotation. About 3 percent of the regeneration harvest volume (46,999 BF/A) would be in white pine. The total volume harvested would be 52,243 BF/A.

Discounted total revenues are \$312.54, and costs \$83.69. Net present value is \$228.85 and benefit/cost ratio is 3.73.

Alternative 3--plant susceptible white pine, Douglas-fir and ponderosa pine. Here the site would have been planted 364 trees per acre white pine (10 percent resistant), Douglas-fir and ponderosa pine. Volunteer grand fir would have brought the stocking to 480 trees per acre today, 44 percent of which would be Douglas-fir, 25 percent grand fir, 19 percent white pine and 13 percent ponderosa pine.

Despite high mortality in the white pine, the thinnings would be able to maintain white pine at about 13 percent of the trees per acre through to rotation. About 14 percent of the regeneration harvest volume (49,161 BF/A) would be in white pine. The total volume harvested would be 52,877 BF/A.

Total revenues are \$325.70, total costs are \$83.69, and the net present value is \$242.01. The benefit/cost ratio is 3.89.

Comparisons. The most obvious contrast is in revenue received from final and intermediate harvests (Table 3). The higher the proportion of white pine, the larger the revenue. This difference results from the higher value of white pine stumpage and from the increased volumes associated with the faster growing, better formed white pine. Even trivial differences in yields, as between Alternatives 2 and 3, generate significant differences in revenues. Wherever differences in revenue are large, differences in benefit/cost ratios are large, because costs for the three alternatives are identical.

A contrast that is not apparent is the reliability of the growth and yield forecasts. Alternative 1 is far more likely to be achieved than either of the other two. Here's why.

TABLE 3

## COMPARATIVE YIELDS AND ECONOMIC BENEFITS

## ULM CREEK SITE

	Alternatives		
	1	2	3
Volume Harvested (BF/A)	59,230	52,243	52,877
Revenue (\$\$)	410.45	312.54	325.70
B/C Ratio	4.90	3.73	3.89

TABLE 4

## COMPARATIVE YIELDS AND ECONOMIC BENEFITS

## ASH CREEK SITE

	Alternatives		
	1	2	3
Volume Harvested (BF/A)	69,977	86,700	56,524
Revenue (\$\$)	451.48	859.95	234.17
B/C Ratio	4.56	8.68	2.36



In Alternative 1, about 91 trees/A are white pine trees. At least 55 of those will be able to survive blister rust, so only 36 trees (40 percent) are subject to the whims of blister rust disease development in the stand over the rotation.

In Alternative 2, about 61 trees/A are white pine, and only 6 are sure to survive blister rust, leaving 55 subject to the whims of the disease. The picture is similar in Alternative 3.

Clearly, overstocking or understocking is far more avoidable for the silviculturist uncertain about the natural fate of 36 of 91 trees than for the silviculturist uncertain about the fate of 55 of 61 trees.

Finally, an unexpected outcome of this analysis was the position of ponderosa pine in the picture. On these south-facing sites, ponderosa pine was just as desirable as white pine; it grows as fast, is just as well formed, and it commands as much stumpage. Indeed, were ponderosa pine seed more abundant in the seed bank, this species would be more strongly featured on these sites.

#### The North-facing Site

This 30-acre site is in the Ash Creek Drainage on a 55 percent slope. The Habitat Type is hemlock/Pachistima, and the productivity is about 130 cu. ft/A/yr. The elevation is 3,200 feet, and the soil is similar to that of the Ulm Creek site.

The site was clearcut and regenerated in 1976. We compare the existing stand with two alternatives, using the same growth and yield and economic comparisons as for the Ulm Creek site. The assumptions common to the three alternatives were the same as those for the Ulm Creek analyses, except:

. The stand is precommercially thinned to 350 trees per acre at age 27 years, and commercially thinned to 120 trees per acre at age 67 years.

Alternative 1--plant white pine 35 percent resistant. This alternative is the existing stand. About 300 white pine trees per acre were planted. Naturals have brought stocking up to 2,654 trees/A today, 49 percent white pine, 42 percent grand fir, 6 percent Douglas-fir and 3 percent western hemlock.

The thinnings and modest mortality (see Appendix 2) in the white pine permit a stand at rotation to consist of 41 percent white pine, 39 percent Douglas-fir, 10 percent western hemlock, and 10 percent grand fir (in trees per acre), yielding 67,377 BF/A, 56 percent of which will be in white pine. The total yield for the stand, including the commercial thinning, will be 69,977 BF/A.

Discounted revenues are \$451.48, and costs are \$99.10. The net present value is \$352.38 and the benefit/cost ratio is 4.56.

Alternative 2--plant white pine 60 percent resistant. This alternative was not available to Wallace in 1976 because of the shortage of stock of this quality. Had it been available, the final proportion of white pine in the stand could have been increased to 66 percent of the trees per acre and the total yield to 86,700 BF/A, including the commercial thinning volume.

Now, the revenue would have been \$859.95, the cost \$99.10 and the net present value \$760.85. The benefit cost ratio would have been 8.68.

Alternative 3--plant Douglas-fir. Had this site been planted during the moratorium, only Douglas-fir might have been planted, at about 300 trees per acre. Naturals would have raised stocking to about 2,700 trees per acre today, 40 percent grand fir, 39 percent white pine, 17 percent Douglas-fir and 3 percent western hemlock. After high mortality in the white pine and two thinnings, the stand at rotation would consist of 84 trees per acre, only 10 of which would be white pine. The stand would yield 52,902 BF/A in the regeneration harvest, plus another 3,622 BF/A in the commercial thinning, for a total of 56,524 BF/A.

The discounted revenue would be \$234.17, the cost \$99.10, and the net present value \$135.07. The benefit/cost ratio would be 2.36.

Comparisons. Alternative 2 (60 percent resistant white pine) is spectacularly the most productive prescription (Table 4) because the proportion of white pine both at final harvest and commercial thinning is so much higher than in either of the other alternatives. In the regeneration harvest in Alternative 2, 66 percent of the trees per acre (i.e. the white pines) yielded 75 percent of the volume. In Alternative 1, 41 percent of the trees per acre were white pines and they yielded 56 percent of the volume. The advantage to increasing the white pine component is clear.

The results of Alternative 3 demonstrate that species other than white pine which are appropriate for these sites are slower growing and display lower form class than white pine, for they do not yield as well when managed similarly in mixed species stands depauperate in white pine. Moreover, none of the alternative species command the stumpage white pine commands, so yield differences are magnified by stumpage differences to generate startling revenue differences.

Again, a contrast not apparent in the analyses (because Prognosis does not very effectively project mortality due to blister rust) is the unreliability of the future stocking estimates for Alternative 3 (and, to a lesser extent for Alternative 1). To avoid overstocking, the silviculturist may count on blister rust killing a high proportion of the 1,053 white pine trees between now and age 27 years. If blister rust fails to kill those trees, the stand may be overstocked.

## Conclusions

For both north- and south-facing white pine sites, increasing the proportion of the white pine component in the stand, without serious over- or understocking, increases revenues and benefit/cost ratios (Tables 3 and 4).<sup>\*</sup> These increases result from:

1. increases in yields due to white pine's faster growth and better form, compared to other species, and
2. stumpage value differences between white pine and other species.

Preventing over- or understocking, however, is more likely when highly resistant stock is planted.

The advantages of western white pine are greater on north-facing slopes than on south-facing slopes because:

1. Its form is better on north-facing than south-facing sites so its proportional yields and stumpage values are greater.
2. The "second best" species on north-facing sites (Douglas-fir) is relatively lower in yields and value than the "second best" on south-facing sites (ponderosa pine).
3. North-facing sites are more productive overall, so percentage yield increases due to white pine magnify absolute increases.

The costs of managing the alternative stands which are reasonable for north-facing sites are quite comparable, but revenues differ spectacularly. For alternatives on south-facing sites, management costs are similar among alternatives, and revenues differ, but not as much as on north-facing sites. South-facing sites are cheaper to manage than north-facing sites, primarily because of lower stocking levels and therefore thinning and final harvest costs. But revenues are substantially lower on south-facing slopes, as well, so the benefit/cost ratios lower for the most productive alternative in Ulm Creek vs. the most productive in Ash Creek.

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<sup>\*</sup> The exception to these results would be stands with a high ponderosa pine component on south-facing slopes; the species grows as well and is as valuable as white pine, but seed supply currently limits its use.

## ECONOMIC ANALYSIS - CHEAPO

A computer program "Computerized Help for the Economic Analysis of Prognosis-Model Outputs" (CHEAPO), has been developed by the College of Forestry, Wildlife and Range Sciences, University of Idaho, to interface with Stage's Growth Prognosis Model. For the Ulm and Ash Creek stands, the CHEAPO economic model was used to undertake an investment analysis of the different alternative management regimes and their associated simulated growth and removal projections.

Discounted costs and revenues from the timber removals were determined and expressed in the output as both net present value (NPV) and a benefit-cost (B/C) ratio.

The CHEAPO model determined the economic feasibility and appeal of different management regimes by computing the harvest year when NPV and B/C ratio for the stand was greatest.

The major base case economic assumptions used in CHEAPO are displayed. They include:

1. Appreciation rate. This real value rate was set at 2.0 percent. This was the average annual rate of stumpage increase for Douglas-fir from 1910-1970.

2. Discount rate. A 4-percent real value rate is currently being used by the Government for public investments and was used in the CHEAPO analysis. A Government study recently found 4-percent to be the real rate of return of new capital investments by private corporations. It therefore represents the opportunity cost of capital from private investors by the tax system.

3. Specifications on the three tree product categories. Large sawtimber, small sawtimber, and poles. By specifying a difference in size classes, value revenues could be determined for each species by tree size.

4. Minimum removal volume 2.5 mbf/acre to be considered a commercial operation.

5. Specified stumpage revenue values by tree product category and species. These stumpage values were obtained using the Idaho Panhandle National Forest's Stumpage Valuation Equation. This equation was developed by regression analysis using data from 65 major timber sales sold on the IPNF.

The Idaho National Forest's Stumpage Value Equation is shown on the following page. The simplified form of the equation, which incorporates a mean number of sale bidders was used. The  $X_4$  dependent variable, shows that stumpage value increases as tree dbh increases. For the  $X_1$  dependent variable, a weighted average lumber

price for all species was not used since the CHEAPO model can take individual species value inputs and will automatically determine total revenues by actual volume removed by species.

The stumpage values calculated by this equation, reflect end-product value after all logging and milling costs, plus a margin for profit and risk have been subtracted.

STUMPAGE VALUE EQUATION  
IDAHO PANHANDLE NATIONAL FORESTS

Regression analysis of 65 sales sold from 12/74 thru 4/80 resulted in the following simplified equation:

$$Y_2 = -287.06 + 0.7743x_1 - 0.5153x_2 - 0.7873x_3 + 80.55x_4$$

where:

- $Y_2$  = high bid value per mbf (first quarter, 1980 \$)
- $x_1$  = species mix weighted average lumber price, L.T. (1st qtr., 1980 \$)
- $x_2$  = percent of sale volume jammer logged
- $x_3$  = percent of sale volume skyline logged
- $x_4$  = the summation of the natural logarithm of each dbh class times the proportion of the total net sale volume in each class (analogous to  $\ln(\text{median dbh})$ ).

This is the equation we will use to calculate stumpage values for the Forest plan. A unique value will be determined for each mix of analysis area characteristics and prescription requirements. The equation is a reduced version of an equation which also includes the following significant variables: market condition, lumber price trend, contract length in months, SBA sales and the number of bidders.

The simplified equation is solved in the following example:

<u>AACharacteristics</u>	<u>Rx Requirements</u>	<u>Lumber Price, LT.</u>
median dbh = 20 inches	logging method = 80% tractor	DF = \$221.50/mbf
species mix = 70% DF	20% jammer	WWP = \$343.33/mbf
30% WWP		
slope = less than 40 %		

$$\begin{aligned}
 Y_2 &= -287.06 + .7743[.70(221.50) + .30(343.33)] - .5153(20) + 80.55[\ln(20)] \\
 &= -287.06 + 199.81 - 10.31 + 241.31 \\
 &= \$143.75/\text{mbf}
 \end{aligned}$$

If we used 100% tractor logging, the value would be \$154.06/mbf; 100% jammer would be \$102.53/mbf; 100% skyline would be \$75.33/mbf.

### Mortality Multiplier Conclusions

Change of MORTMULT to .5 - Decreases mortality too significantly resulting in unreasonably high BF vol. (93,000 BF @ 90 years), PAI (451 ft.<sup>3</sup>/ac./yr.), BA/A.

Change of MORTMULT to 2 - Doubles mortality too significantly, only 2 percent of the WP make it through the 90 year projection. (25 WP out of 1300).

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Baseline mortality rate of 1, represents well a stand of WP planted w/35 percent BRR stock.

321 WP planted → Expect 110 WP @ rot.

1300 WP total (includes 321 planted/ac.) → 169 WP @ rot.

Additional 59 due to 10 percent resistance of remaining 979 natural WP.

To simulate BR, mortality on 60 percent BRR stock of WP planted - change mortality rate, MORTMULT to .75.

Total of WP @ end of rot. will not = 60 percent of planted WP and 10 percent of natural WP due to other mortality factors such as suppression, max BA.

i.e. Begin 1300 WP - 321 60 percent BRR 979 natural.  
End w/256 WP from 366 T/A @ rot.

With/321 planted → Expect  $\hat{=}$  190 @ 60 percent resis.  
979 naturals → Expect  $\hat{=}$  100 @ 10 percent resis.

or

256 vs. 290

---

To simulate BR mortality on nursery-run (millrun) WP change MORTMULT Increase it to 1.60.

A change of 1.75 yields only 3 percent resistance, or 44 WP from 1300.



Ulm Creek, Alt.#1 - 60% BRR WP,DF,PP

Begin 480 T/A      44% DF → 211 T/A  
                    25% GF → 120 T/A  
                    19% WP → 91 T/A  
                    13% PP → 62 T/A

Col. MAI            Precommercial thin not needed since only 326 T/A page 24  
@ 100 yr.           (2002).

projection  
2082                Commercial thin to 100 T/A @ 2042 (age 44).

At Rot. 78 T/A      46% DF → 36 T/A  
                    30% WP → 23 T/A  
                    19% PP → 14 T/A  
                    5% GF → 4 T/A

Commercial thin vol. 5,808 BF    76% DF  
   14% WP  
   8% PP  
   2% GF

Regen. harvest vol. 53,442 BF    44% DF → 23,505  
   31% WP → 16,560  
   22% PP → 11,752  
   3% GF → 1,602

Total harvest vol. 59,230 BF

Median DBH = 22.7", Quad X DBH = 24.6"

ULM CREEK ALTERNATIVE #2 ONLY DF PLANTED w/WP,PP Nat.

Begin w/510 T/A      59% DF → 300 T/A  
                         18% GF → 92 T/A  
                         12% WP → 61 T/A  
                         12% PP → 61 T/A

Cul. MAI.  
@ 100 YR.      No precommercial thin. only 335 T/A @ 2002 comm. thin to  
project      100 T/A @ 2042 (age 64).  
2082.

At rot. 76 T/A      73% DF → 55 T/A  
                         23% PP → 17 T/A  
                         3% WP → 2 T/A  
                         1% GF → 1 T/A

Comm. thin. vol. 5244 BF      85% DF  
   10% WP  
   5% PP  
   1% GF

Regeneration harvest vol. 46,999 BF      68% DF = 31,959  
   28% PP = 13,159  
   3% WP = 1,409

Total harvest vol. 52,243 BF

Median DBH = 23.5"      Quad  $\bar{x}$  DBH = 20.2

\* Could change SPECREF. on WP to 2 to ↑ thinning of WP? Or eliminate DF  
PREF.

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ULM CREEK, ALTERNATIVE #3 - Nursery Run WP w/DF + PIPO

Begin 480 T/A	44% DF →	211 T/A
	25% GF →	120 T/A
	19% WP →	91 T/A
	13% PP →	62 T/A

Cul. MAI. Precomm. thin not done only 244 T/A @ 2002 (age 24)

@ 100 Yr. projection 2082 Comm. thin to 100 T/ A @ 2042 (age 64)

At rot. 75 T/A	65% DF →	49 T/A
	18% PP →	14 T/A
	13% WP →	10 T/A
	4% GF →	3 T/A

Comm. thin. vol. 3,716 BF 62% DF  
20% PP  
11% WP  
7% GF

Regen. Harvest vol. 49,161 BF	59% DF =	29,004 BF
	24% PP =	11,798 BF
	14% WP =	6,882 BF
	3% GF =	1,475 BF

Total Harvest vol. 52,877 BF

Median DBH = 22.8"

Quad.  $\bar{x}$  DBH = 24.8"

ASH CREEK, ALTERNATIVE #1 (35% BRR WP)

Begin 2654 T/A	→	49% WP	=	1300 T/A
	→	42% GF	=	1114 T/A
	→	6% DF	=	160 T/A
	→	3% H	=	80 T/A

Cul. MAI  
@ 100 Yr.  
projection  
2082

Precomm. thin to 350 T/A @ 2002 (age 27)  
Comm. thin to 120 T/A @ 2042 (age 67)

<u>At rot.</u>	85 T/A	→	41% WP	→	35 WP
			39% DF	→	33 DF
			10% WH	→	8 H
			10% GF	→	9 GF

Comm. thin. vol. 2,600 BF	→	78% WP
		18% GF
		3% H
		1% DF

Regeneration Harvest vol.	67,377 BF	→	56% WP	=	37,731
			32% DF	=	21,560
			6% WH	=	4,042
			6% GF	=	4,042

Total harvest vol. 69,977 BF

Median DBH = 23.1",      Quad.  $\bar{x}$  DBH = 24.4"

ASH CREEK, ALTERNATIVE #2 (60% BRR.)

Begin	2654	T/A	49%	WP	➡	1300	T/A
			42%	GF	➡	1114	T/A
			6%	DF	➡	160	T/A
			3%	H	➡	80	T/A

Cul. MAI

100 Yr. Proj.

Year 2082      Precommercial thin to 350 T/A @ 2002 (age 27)  
Comm. thin to 120 T/A @ 2042 (age 67)

<u>At rot.</u>	92 T/A	66% WP	61 T/A
		27% DF	24 T/A
		5% WH	5 T/A
		2% GF	2 T/A

Comm. thin. vol. 11,292 BF      94% WP  
   4% DF  
   2% GF  
   1% WH

Reg. cut volume	75,408 BF	75% WP =	56,556 BF
		21% DF =	15,836 BF
		2% WH =	1,508 BF
		1% GF =	754 BF

Total harvest volume = 86,700 BF

Median DBH = 23 inch      Quad.  $\bar{x}$  DBH = 24"

ASH CREEK ALTERNATIVE #3 (assume DF)

Begin 2700 T/A      40% GF → 1080 T/A  
                         39% WP → 1053 T/A  
                         17% DF → 459 T/A  
                         3% H → 81 T/A

Cul. MAI  
@100 yr.              P.comm. thin. to 350 T/A @ 2002 (age 27)  
proj. 2082            comm. thin to 120 T/A @ 2042 (age 67)

At. rot.              84 T/A    70% DF    59 T/A  
                                 12% WP    10 T/A  
                                 10% WH    8 T/A  
                                 8% GF    7 T/A

Comm. thin volume = 3,622 BF              41% WP  
   37% DF  
   20% GF  
   2% WH

Regen. cut volume 52,902 BF              65% DF = 34,386  
   19% WP = 10,051  
   9% WH = 4,761  
   7% GF = 3,703

Total volume harvested = 56,254 BF/AC.

Median DBH = 23"    Quad.  $\bar{x}$  DBH = 24"

BA ↓ to 187 ft<sup>2</sup>/ac. after thin., good!

## Appendix 4

### Prognosis Runs

(Printouts included in original only.)  
(Contact author, Howe)

## Appendix 5

### CHEAPO Runs

(Printouts included in original only.)  
(Contact author, Howe)



Some Genetic Considerations  
in the  
Maintenance and Enhancement of Balance  
in  
Host-pest Systems  
by  
Peter A. Theisen, Regional Geneticist

A. Introduction. The following definitions are given to establish the meanings of words and terms as used in this paper.

Host - A plant or animal from which a pest gains sustenance.

Pest - An organism that derives sustenance from another organism without making compensation.

Host-pest system - The relationships and interactions, between a host and a pest including environmental factors that affect these relationships and interactions. These environmental factors include climate, other members of the community including the pest's pests and so on down through the trophic levels, nutrition, etc.

Region 6 is currently involved in five pest resistant programs which include the following host-pest systems:

Western white pine - white pine blister rust

Sugar pine - white pine blister rust

Port-Orford cedar - Phytophthora lateralis root rot

Lodgepole pine - western gall rust

Douglas-fir - blacktail deer

These resistance programs serve approximately 2,000,000 acres of R-6 commercial forest land, which is about 1/8 of the R-6 commercial forest land covered by tree improvement programs, and only a portion of one host-pest system for each of these species. It is readily apparent that

these resistance programs cover only a very small portion of the host-pest systems of commercial forest tree species in the Pacific Northwest.

"The objective of tree improvement is to produce increased quantities per unit area of higher quality forest products" (U. S. Forest Service, FSM 2475, 1977). To meet this objective these increases need to be stable overtime. A major area of concern is our ability to maintain or enhance host-pest systems in tree improvement programs in which these systems are indirectly addressed.

Knowledge gained from our involvement in resistance programs should be of considerable value in guiding our indirect approach in the management of other host-pest systems as part of our tree improvement programs. We also need to look to the past to gain some insight into how the host-pest systems developed, make correlations to the present, and projections into the future based on these observations.

We have entered an era of intensive management of commercial forest land to enhance timber yields in the absence of major reliance on the use of pesticides. The option of letting nature run her course in these systems is no longer available. Disregarding them will not keep them out of sight and will adversely affect the goal of intensive management. The only viable option is to make sure that host-pest systems are adequately addressed in management decisions.

Despite the fact that our current knowledge of the interactions of host-pest systems operating in our commercial forest species is limited at best for some systems and for most non-existent there are general principles that can be garnered from evolutionary theory, forestry, crop science, behavioral genetics, population genetics, genecology, plant pathology, entomology, resistance breeding, etc., that if applied should keep us out of serious trouble and allow us to respond to new information as it becomes available.

## B. The Past.

1. Coevolution of Host-pest Systems. Coevolution is the simultaneous evolution of interacting populations (Roughgarden, 1979). Coevolution may result in symbiotic relationship between two or more individuals of different species or in complex associations not involving symbiosis in which each species pursues its own evolutionary strategy. Kinds of symbiotic relationships are parasitic, commensal, and mutualistic. There is evidence that coevolution between members of a community tends to structure genetic materials into highly interacting coadapted gene complexes so that those genotypes that confer higher fitness occur more frequently in the population than if the genes acted independently (Clegg, et al., 1972).

Host-pest system relationships do not remain stable over evolutionary time, neither can they be considered stable in space or in the degree that the coadaptation is based on symbiotic or non-symbiotic relationships or various combinations between these types of relationships. The response of a host and a pest to environmental factors not directly affecting interactions between them can affect the equilibrium in the host-pest relationships (Roughgarden, 1979). Coevolution can take place gradually over time, or in a stepwise pattern (rapid change separated by periods of gradual change), or in a single rapid change (Stanley, 1979).

Palaeobotanical evidence of plant defense mechanisms against other organisms in the ecosystem indicates that the coevolution of green plants and their pests dates back at least 400 million years (Harborne, 1977). It is generally accepted that when the gene center of the host is also the center of origin of its specialized pest that coevolution has continued through time unless interrupted by the separation of host and pest (Leppik, 1970).

During adaptive radiation from their original gene centers, plants may leave behind their specialized pests, coevolution may proceed differently than in the original gene center, the plant and the pest may evolve along different pathways and become separated, either the plant or the pest may

become extinct, the plant may pick up new pests, or the plant may again come in contact with pests or pest relationships left behind in the past. In addition, the pest may leave some or all of its pests behind or may pick up new pests, etc.

The trend in coevolution of host-pest systems is toward homeostasis or balance (Pimental, et al., 1963; Pimental and Al-Hafidh, 1965; Pimental, 1968). The main factor involved in the evolution toward homeostasis is considered to be host-pest interactions that change the reproductive capacity of the pest. This change results in a decrease in the density of the pest population, a decline in the selective pressure on the host, and dampening of fluctuations in the pest population (Pimental and Al-Hafidh, 1965).

Homeostasis among members of a community results in improved survival of the community, is partly responsible for increased species diversity in the community, which in turn contributes further to community homeostasis (Pimental, 1968; Wittaker, 1972). According to Stanley, 1979, moderate predation permits diversity to evolve while intense predation may lead to widespread extinction and a decline in diversity. Refer to Roughgarden, 1979, for a significant discussion that species diversity does not necessarily contribute to community stability but rather increases the likelihood of species extinction as the community becomes more complex and interdependent. These views are not contradictory since the key to the effects of species diversity is the degree of interdependence between two species in the community. If interdependence between two species is complete, the extinction of one species results in the extinction of the species dependent upon it for survival. For host-pest relationships to persist in a community there has to be some degree of equilibrium between the host and the pest.

Maximum fitness in the present environment and adaptability to future environments are generally considered to be opposing forces on plant populations which have led to a compromise between present and future fitness for evolutionary survival (Barber, 1958; Heslop-Harrison, 1966; Nienstaedt, 1976; and Thoday, 1953).

Coadaptation through natural selection in the coevolution of host-pest system is expected to lead to nonoptimal present fitness in both host and pest (Roughgarden, 1979). At coevolutionary equilibrium:

- a. The host underdefends.
- b. Increasing host defense will cause increasing pest searching effort to evolve.
- c. The pest searches too hard.

In a general review of coevolution of host-parasite systems in forest ecosystems Stern and Roche, 1974, emphasized the following points:

- a. There is no sharp distinction between parasites and saprophytes.
- b. It is possible for a parasite to produce and try 100 generations during one generation of the host.
- c. Stability is hardly possible if the host is a tree in a simple gene-for-gene host-parasite system based on major genes of the R and V type. Refer to Knott, 1972, and Section C of this paper for some qualifications.
- d. Selection of resistant forms in old host-parasite systems could disturb the established natural equilibrium, but selection of resistant forms in young host-parasite systems could lead to equilibrium.
- e. Pests may be locally adapted to specific weather cycles and environmental extremes of specific localities.
- f. In host-parasite systems there is a multitude of biochemical, physiological, and ecological variations.

2. Human Experience. There is a great deal of background information available concerning host-pest relationships in crop plants and information concerning host-pest relationships in forest trees is accumulating. Various speakers at this workshop have covered the current concepts of host-parasite relationships and interactions, resistance breeding, deployment of resistance, and integrated pest management techniques.

Roger Sandquist and Jim Hadfield have discussed off-site planting of forest trees and the loss of equilibrium in some host-pest systems associated with this practice. Management practices that lead to large buildups in pest populations can affect the rate of damage, increase plant exposure to mutant forms and genetic combinations of pests that can overcome or reduce existing resistance (Day, 1974; Johnson, 1961), and thus destabilize host-pest systems in adjacent populations.

3. The Lessons From the Past are:

a. The large number of extinct species provides overwhelming evidence that the evolutionary strategy of a species is seldom optimum for the species.

b. Models of host-pest relationships are useful in contributing to our understanding of these relationships but are usually over-simplifications of what actually occurs.

c. The response of a host and a pest to environmental factors not directly affecting interactions between them can affect the equilibrium in host-pest systems.

d. Continued coevolution of a host and a pest may occur as a rapid change (a catastrophic event in human terms) as part of a stepwise pattern of coevolution.

e. The trend in coevolution of host-pest systems is toward balance.

f. The maintenance of moderate predation in host-pest systems appears important in maintaining equilibrium in the system.

g. The trend toward balance in host-pest systems is not possible if the pests do not track geographic variations in the host that affect host-pest interactions.

h. Perfect balance in a host-pest system implies that coevolution of the system is static. This condition may be evolutionary disadvantageous for both host and pest.

i. Interactions and relationships in host-pest systems can vary in space and time.

j. The occurrence of host-pest systems in a specific host population can vary in space and time.

C. The Present. The opportunities for using natural resistance and resistant genotypes in forest management are limited to those programs in which host-pest interactions are reasonably understood and in which resistant genotypes are identified. The term use implies that we are going to put natural resistance into action or service which may be done in resistance programs but for the most part we will be trying to maintain or possibly enhance existing natural resistance and not leave it behind or drastically change it as tree improvement programs progress.

How forest tree populations are managed will guide the evolution of their associated pest systems.

Controlling the origin, identity, and use of forest reproductive material has long been recognized as a key management item (Baldwin, 1933; Eckbo, 1916; Frankhausen, 1931; Pearson, 1914; and Pinchot, 1908). However, even today, forest reproductive material use guidelines are biologically poorly defined and none adequately address a species geographic variation pattern and that of its pests and the pest's pests etc., down through the

trophic levels. In Region 6, the control of the origin and identity of forest reproductive material from harvest through use by State certification agencies is a recent development not yet fully implemented in the use phase on all National Forests.

As part of our tree improvement program, we are now installing a series of evaluation plantations involving short and long range movements of forest reproductive material, nursery tests, and controlled environment tests; we are actively supporting research on geographic variation by making forest reproductive material readily available to researchers; and are involved in biochemical assays which will produce much useful information. At present, we are trying to be conservative in our tree improvement programs and forest reproductive material use guidelines so that we will retain the foundation for optimum use of this information.

The host-parasite system with which we have the most experience is the western white pine-white pine blister rust system. Since 1956 the Region has been involved in a resistance breeding program involving this system. Clear evidence of geographic variation has been found in white pine blister rust in Region 6 and this has been recently verified in a research study.

Currently we have a problem with parasites on blister rust cankers at our rust screening facility which has seriously affected our ability to screen for certain types of resistance. Indeed, if these parasites are as effective in the forest as they are at Dorena there would be no need to breed for resistance to white pine blister rust. Maybe we should really be using the screening facility to produce more virulent populations of Fusarium and Tuberculina for introduction into white pine stands in which blister rust is a problem. Evidence indicates that canker inhabiting fungi are already driving the white pine-white pine blister rust system toward balance (Hungerford, 1977; Kimmey, 1969). Perhaps we can hasten this development by deploying more virulent strains of these canker inhabiting fungi. Stability in a system based on major R and V type genes is possible in this situation.



Even though a pest of a forest tree species may be able to produce and try a large number of generations during one generation of the host, forests can be managed to offset this apparent pest advantage. Indeed, the evidence indicates that there is no advantage to the pest based on this generation cycling disparity. Granted, there are outbreaks of native pests but these outbreaks in historical times have dropped to pre-outbreak levels at an extremely rapid rate in terms of evolutionary time. During a rotation, a tree is not uniformly available to a pest. As a tree grows from a seedling to a mature tree physiological changes take place in the tree, the tree occupies different environments, and the forest community also changes.

Current management direction in Region 6 includes the following items that have been identified as useful tools in reducing the build-up and thus the impact of native pests.

- a. Long distance movement of forest reproductive material from place of origin is avoided in forestation programs.

- b. A conscientious effort is made to maintain adaptive genetic diversity in local populations.

- c. The primary regeneration systems used in the Region avoid large continuous areas of even aged forests. Non-commercial forest land, modified management areas in the CFL base, and protected reserves such as wilderness areas, etc., adds to the diversity between forests stands.

- d. Mixed species stands are encouraged.

- e. Stands under management are maintained in a thrifty condition.

- f. Natural regeneration even on planted areas is encouraged.

- g. Site specific silvicultural prescriptions are made to replace unthrifty stands with tree species suitable to the site.

D. The Future. The past and present shape the future. How well we manage host-pest systems now will affect the future equilibrium in the systems.

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INTEGRATED PEST MANAGEMENT DECISION KEY:  
A NEW DECISION-MAKING TOOL FOR THE FOREST MANAGER

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Abstract.--The Integrated Pest Management Decision Key (IPM-DK) is a "user-friendly", interactive, computer program listing management options for southern pine beetle, annosus root rot, littleleaf disease, fusiform rust, brown spot, and pales weevil on southern pines. The program considers a variety of environmental, economic, geographic, and other recommendations. Specific guidelines are provided on the use of improved seedlings for fusiform rust and brown spot resistance.

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### INTRODUCTION

Forest land managers have long used a variety of preventive and direct control options to deal with specific forest pests, but only recently have we begun to consider the multiple interactions of insects, diseases, treatments, and stand conditions on the forest. Host, pest, and treatment dynamics are complex. Yet, these relationships are the basis for developing and implementing "integrated pest management."

Integration is what management is all about at both the stand and forest level. Silviculturists and managers are becoming more aware of what pests are costing in terms of growth, yield, dollars, or whatever their objective. Pests are being considered more than ever in the planning and implementation of silvicultural and management activities. Guidelines are available to help the silviculturist and manager integrate pest conditions into the decision-making process. Silviculturists and managers are helping to formulate these guidelines.

In recent years, we have seen many new recommendations and approaches to insect and disease management. These recommendations have been published in many forms. Newsletters, handbooks, flyers, pamphlets, journal articles, and extension bulletins are just a few examples. The resource manager has had to sort through a variety of publications to find the recommendations, and then select the most relevant information for a particular tract of land.

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There are always questions, such as: "Do I have the most current information? Will it work on my 100 acres? What about other pests? Where is the best place to put my genetically improved seedlings?" In some cases, control and prevention recommendations for one pest may conflict with those for another. For example, drainage of wet areas to discourage southern pine beetle buildup may increase susceptibility of the stand to annosus root rot during subsequent thinnings.

This Integrated Pest Management Decision Key (IPM-DK) has been developed to help resolve these conflicts and provide the resource manager with current, recommended, management options in an easily understood form. Only proven and practical procedures are contained in the key.

#### HOW THE IPM-DK WORKS

The IPM Decision Key is an interactive computer program which lists management options for southern pine beetle, fusiform rust, annosus root rot, littleleaf disease, brown spot, and pales weevil in loblolly, slash, shortleaf, and longleaf pine stands. In addition to pest-host interactions, the program also considers environmental, geographic, and economic factors which influence management decisions.

The user should have the IPM-DK User's Manual, which clarifies and elaborates on the output. Copies are available from:

IPM-DK Coordinator  
Forest Pest Management, S&PF  
USDA Forest Service  
1720 Peachtree Road, N.W., Room 710  
Atlanta, GA 30367

It is important to have the most current version of the user's manual because it will continue to be modified with the most up-to-date information relating to other pests, other management units, and research findings. The current version number will be indicated at the beginning of the decision key printout.

The IPM-DK analysis starts with inputs of information usually known to the user. Figure 1 lists the basic information needed to complete a stand analysis. Supplemental information can also be added to help the manager accept or reject recommendations provided by the key. As indicated in the example, the resource objective is solid wood products on a 35-40 year rotation; southern pine beetle, fusiform rust, and annosus root rot are the pests being considered, and the stand is being regenerated. The site is high-hazard (as defined in the manual) for southern pine beetle and fusiform rust, but not for annosus root rot, and southern pine beetle is not present. Sixty-five percent of the trees in the adjacent stand are infected with fusiform rust. The stand is located in the Coastal Plain.

A quick look at the supplemental information shows that fusiform rust is the most serious, potential problem for the newly established stand. The southern pine beetle could be a problem later in the rotation.

At this time, the program would be accessed by calling an Apple® computer of the USDA Forest Service, Forest Pest Management group in Doraville, Georgia. The commercial number is (404) 221-5200. The user must have an interactive terminal which is set at 30 characters per second (300 BAUD) and full duplex. Upon contacting the computer, the user will be presented with descriptive procedures relating to the IPM-DK. The questions are straightforward and answered with a one-character response, such as:

- Y - Yes
- N - No
- B - Backup. Allows the user to have the last question asked again.
- E - Exit. Allows the user to start over or to terminate the session.
- R - Allows the user to print a complete recommendation.
- D - Allows the user to print a list of all recommendations.

The following example uses the information in figure 1.

```
0010    DO YOU WANT TO CONSIDER SOUTHERN PINE BEETLE? Y
0020    DO YOU WANT TO CONSIDER FUSIFORM RUST? Y
0030    DO YOU WANT TO CONSIDER ANNOSUS ROOT ROT? Y
0040    DO YOU WANT TO CONSIDER LITTLELEAF? N
0050    IS THIS MANAGEMENT UNIT A FOREST STAND? N
0060    IS THIS MANAGEMENT UNIT A SEED ORCHARD? B
0050    IS THIS MANAGEMENT UNIT A FOREST STAND? Y
0100    IS THIS AREA TO BE REGENERATED WITHIN THE NEXT 10 YEARS? Y
0370    ARE YOU GOING TO REGENERATE WITH LONGLEAF? N
0260    IS THE AREA TO BE NATURALLY REGENERATED AS OPPOSED TO PLANTED? N
0320    DO YOU WANT TO CONSIDER PALES WEEVIL? N
0142    ARE CONDITIONS HIGH HAZARD FOR SOUTHERN PINE BEETLE? Y
0144    ARE CONDITIONS HIGH HAZARD FOR FUSIFORM RUST? Y
0146    ARE CONDITIONS HIGH HAZARD FOR ANNOSUS ROOT ROT? N
0150    IS MORE THAN 50% OF THE SITE OR ADJACENT STANDS INFECTED WITH
        FUSIFORM? Y
0160    IS THIS MANAGEMENT UNIT IN THE COASTAL PLAIN? N
0170    IS THIS MANAGEMENT UNIT IN THE PIEDMONT? N
0180    IS THIS MANAGEMENT UNIT IN THE MOUNTAINS? N
```

One of the last 3 questions has to be answered yes...Try again...

```
0160    IS THIS MANAGEMENT UNIT IN THE COASTAL PLAIN? Y
```

SOUTHERN PINE BEETLE-LOBLOLLY, SLASH, SHORTLEAF ONLY

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R18    CONSIDER ALTERING PLANTING DENSITY.
R30    MANAGE SPECIES COMPOSITION.
R31    REGULATE AGE CLASSES.
R32    DRAIN WET SITES.
R33    AVOID DAMAGE TO LOW LYING AREAS.
R34    INTENSIFY MANAGEMENT ON GOOD SITES.
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FUSIFORM RUST-LOBLOLLY, SLASH ONLY

- R11 WHEN AVAILABLE, USE SEEDS OR SEEDLINGS WHICH ARE RESISTANT TO THE PEST.
- R13 CULL SEEDLINGS WITH FUSIFORM SWELLINGS ON THE STEM.
- R14 REDUCE OAK POPULATION WHEN PRACTICAL AND WHEN NOT IN CONFLICT WITH OTHER MANAGEMENT PRACTICES.
- R15 MODIFY FERTILIZATION PRACTICES.
- R18 CONSIDER ALTERING PLANTING DENSITY.
- R30 MANAGE SPECIES COMPOSITION.
- R31 REGULATE AGE CLASSES.

ANNOSUS ROOT ROT-LOBLOLLY, SLASH, SHORTLEAF ONLY

- R00 NORMAL MANAGEMENT.

Additional information can be requested for any of the pest management options. The following example is for using resistant seedlings for fusiform rust:

- R11 WHEN AVAILABLE, USE SEEDS OR SEEDLINGS WHICH ARE RESISTANT TO THE PEST.

FUSIFORM RUST-LOBLOLLY, SLASH ONLY

WHEN POSSIBLE, AVOID PLANTING RUST-SUSCEPTIBLE PINES ON HIGH-HAZARD SITES. REGENERATION OF HIGH-HAZARD SITES SHOULD BE DONE WITH SEEDS OR SEEDLINGS FROM;

RUST RESISTANT SLASH AND LOBLOLLY PINE SEED ORCHARDS, OR

GEOGRAPHIC AREAS OF RESISTANCE: E.G., LIVINGSTON PARISH, LA., EAST TEXAS, MARYLAND, ARKANSAS, ETC., OR A MIXTURE OF THESE. USE RESISTANT LOCAL SOURCES WHEN POSSIBLE.

- 0200 DO YOU WANT MORE INFORMATION ON A PARTICULAR RECOMMENDATION? D

A complete list of options can be obtained by entering a "D":

ALL POSSIBLE RECOMMENDATIONS

- R00 NORMAL MANAGEMENT.
- R11 WHEN AVAILABLE, USE SEED OR SEEDLINGS WHICH ARE RESISTANT TO THE PEST.
- R12 USE PROTECTIVE CHEMICAL TREATMENTS WHEN ECONOMICAL.
- R13 CULL SEEDLINGS WITH FUSIFORM SWELLINGS ON THE STEM.
- R14 REDUCE OAK POPULATION WHEN PRACTICAL AND WHEN NOT IN CONFLICT WITH OTHER MANAGEMENT PRACTICES.
- R15 MODIFY FERTILIZATION PRACTICES.
- R16 PRUNE AND EXCISE FUSIFORM RUST GALLS AND CANKERS.
- R17 CONSIDER THINNING OR SALVAGE CUTTING.
- R18 CONSIDER ALTERING DENSITY OF PLANTING.
- R19 CONSIDER SEED TREE OR SHELTERWOOD REGENERATION.
- R20 CONSIDER SUBSOILING.

- R21 CONSIDER PRESCRIBED BURNING.
- R22 PERFORM FREQUENT SURVEILLANCE.
- R23 TREAT STUMPS WITH PHLEBIA GIGANTEA.
- R24 TREAT WITH BORAX OR THIN DURING SUMMER (MAY-AUGUST) SOUTH OF 34 DEGREES NORTH LATITUDE.
- R25 CONSIDER IRRIGATION.
- R26 CONTROL ACTIVE INFESTATIONS.
- R27 REMOVE HIGH RISK TREES.
- R28 MINIMIZE SITE DISTURBANCE.
- R29 AVOID DAMAGE TO TREES.
- R30 MANAGE SPECIES COMPOSITION.
- R31 REGULATE AGE CLASSES.
- R32 DRAIN WET SITES.
- R33 AVOID DAMAGE TO LOW-LYING AREAS.
- R34 INTENSIFY MANAGEMENT ON GOOD SITES.
- R35 HARVEST AT AGE 25.
- R36 NO CHEMICAL TREATMENT NEEDED NOR DELAY IN PLANTING. PLANT SEEDLINGS IN DECEMBER THROUGH FEBRUARY.
- R37 ALLOW SITE TO REMAIN IDLE 1 YEAR. PLANT SEEDLINGS NEXT PLANTING SEASON.
- R38 AVOID PLANTING SEEDLINGS IN AREAS NEXT TO LARGE SUMMER OR FALL CLEARCUTS.
- R39 REMOVE SEED TREES OR SHELTERWOOD AT AGE 1-2.

Detailed information can be obtained for any of the options. An example for using seedlings resistant to brown spot follows:

- R11 WHEN AVAILABLE, USE SEEDS OR SEEDLINGS WHICH ARE RESISTANT TO THE PEST.

#### BROWN SPOT-LONGLEAF ONLY

PLANT RESISTANT SEEDLINGS OR (IF LACKING THOSE) HIGH-QUALITY, LONGLEAF SEEDLINGS ON INTENSIVELY PREPARED SITES. GET SEEDLINGS ONLY FROM NURSERIES THAT MAINTAIN SEEDBED DENSITIES AT 10 TO 15 SEEDLINGS PER SQUARE FOOT (929 SQUARE CM) AND PRODUCE DISEASE-FREE SEEDLINGS BY SCHEDULING FUNGICIDE TREATMENTS UP TO THE TIME OF LIFTING.

The forest managers now have to decide if the pest management recommendations apply to their particular stand or forest conditions. No "standard" treatments will apply to all situations. Each management unit, forest condition, and resource objective presents different management problems. Each might require a different combination of methods to reduce damage from pests.

A check of the options shows that annosus root rot is not expected to be a problem throughout the life of the stand. Southern pine beetle may become a problem in later years. The IPM-DK is providing prevention techniques that may reduce the future risks. Southern pine beetle options 32 (DRAIN WET AREAS) and 33 (AVOID DAMAGE TO LOW LYING AREAS) do not apply to this area. Options 30 (MANAGE SPECIES COMPOSITION) and 31 (REGULATE AGE CLASSES) are good concepts, but are rejected because the decision to plant this year to loblolly pine cannot be changed. Options 18 (CONSIDER ALTERING PLANTING DENSITY) and 34 (INTENSIFY MANAGEMENT ON GOOD SITES) should be implemented.

For fusiform rust, option 15 (MODIFY FERTILIZATION PRACTICES) does not apply, since fertilization was not planned. Options 30 and 31 do not apply for the same reason used for southern pine beetle. The remaining four options do apply and will be used in the stand prescription.

After eliminating some of the obvious recommendations that do not apply to this particular situation, the decision-making becomes more difficult. This is where economics, management philosophy, and experience may come into play.

Because of the high hazard for fusiform rust, the use of site preparation techniques that minimize oak reproduction, culling infected seedlings, and using resistant seedlings appear to be the most important considerations. The option to consider altering planting density says to increase the number of trees per acre for fusiform and decrease the number for southern pine beetle. Considering that fusiform rust will kill some of the seedlings, a planting density of 650 trees per acre was selected. If enough seedlings are lost to fusiform, the stand will not become overstocked, and the hazard for southern pine beetle remains low. However, if the losses to fusiform are low, the stand would be set up with a thinning program designed to reduce the southern pine beetle hazard under option 34 (INTENSIFY MANAGEMENT ON GOOD SITES).

The IPM Decision Key was not developed to dictate the course of management action. Prevention and control recommendations have to be weighed against economic and environmental considerations to determine how stands are managed. The IPM-DK does allow us to better integrate insect and disease considerations into the decision-making process.

#### WHAT DOES THE FUTURE HOLD?

A variety of additions are on the drawing board. Some of these are:

- Brown Spot
- Reproduction Weevils
- Nurseries
- Seed Orchards
- Hardwood Pests
- Urban Tree Pests

Additionally, a user center is planned, where anyone can send a completed form to a central facility and receive a printout through the mail. Eventually, specific economic inputs (such as product value and labor cost) will help ensure that pest management options are cost effective.

We feel that we are on the threshold of a new and innovative system. The computers are here to stay; terminals are more readily available; and a substantial amount of technology is ready for transfer. Therefore, it seems that a system of this type, which includes all of the major pests and tree species, would be a very valuable aid to the forest manager.

INTEGRATED PEST MANAGEMENT DECISION KEY  
Stand, Site, and Pest Information

Information Needed for IPM-DK

1. Pest to be considered (check one or more)

Southern Pine Beetle X  
Fusiform X  
Annosus Root Rot X  
Littleleaf     

2. Pest management unit (check one or more)

Forest Stand X  
Seed Orchard       
Shade Trees       
Nurseries       
Other Areas     

3. Stand status (check only one)

Area to be Regenerated x  
    Natural?       
    Planted? x  
2 inches or less       
2 inches or mature X  
Overmature     

4. Hazard rating (check one or more)

High Low

Southern Pine Beetle X       
Fusiform X       
Annosus Root Rot      X  
Littleleaf      X

5. Geographic Location (check only one)

Coastal Plain X  
Piedmont       
Mountains     

6. Annosus Root Rot (Trees off-color, thin crowns, tufted foliage, and/or fruiting bodies) (check only one)

Present       
Absent X

Supplemental Information

1. Management objective

Solid Wood Products

2. Stand conditions

Age (years) 0  
Basal area 0  
Site index 85 (Previous Stand)  
No. of trees/A 650 (To be Planted)  
Avg. d.b.h. 0  
Avg. height 0  
Rotation age 35-40

3. Pest conditions

SPB active       
    inactive X

Fusiform rust

% stems infected in stand or adjacent stand 65

Annosus root rot

% stems showing disease symptoms in stand or adjacent stand 0

4. Other

Loblolly Pine Plantation

Figure 1.--Basic information necessary to complete a stand analysis.

# USE OF BLISTER RUST RESISTANCE

by

Geral I. McDonald

## Introduction

Plant disease epidemics have been described as a "host-pathogen system out of genetic balance in favor of the pathogen" (Browning et al. 1977). The white pine blister rust epidemic of North America fits this description well. Blister rust epidemics operate on the same principals as do the epidemics of full cycle rusts on cereal grains. Study of these epidemics by agriculturists clearly demonstrates that management of rust epidemics is a problem in gene management. Of equal importance are the economic host gene pool, the pathogen gene pool, and the gene pool of any alternate hosts. Application of these gene management techniques requires a thorough understanding of the epidemiologic relationships of the target disease. All avenues of control must be utilized in a well planned and integrated effort to bring the system back into "genetic balance". This genetic balance is still an elusive and ill defined condition for most all host-pathogen systems, but study of wild "balanced" systems can supply some benchmarks. First, heterogeneity seems to be a key ingredient. Secondly, environmental effects are totally interwoven into the interaction.



Third, complex, genetically heterogenous systems supply more management pressure points than do simple systems but at the same time they require more sophisticated knowledge. Fourth, out of balance systems will eventually find their own balance in the absence of man's influence. The key to successful integrated blister rust management is to increase the rate of movement toward the "balanced" state without destroying the essential elements of the natural interaction. Our design objective as stated by Offord in 1956 is "to reduce blister rust to the status of a minor pest," and keep other pests in their minor status.

I will describe a proposed program of blister rust management for western white pine, including both natural and artificially selected populations, that should accomplish this objective. The program is based on four principals: (1) maximize genetic breadth of white pine through resistance-hazard alignment and widespread planting of a highly heterogenous population of pine; (2) minimize the number of alternate hosts in all stands and increase the level of their resistance to rust; (3) refrain from application of total selection pressure on the rust; and (4) make all management decisions to harmonize control options. The list of control options include multiple levels of usable resistance, control of pine growth rates, stocking density, ribes surveys (plants), ribes surveys (seeds), mixed species plantings, control of planting stock size, cutting practices, logging and site preparation methods (non-disturbance logging and controlled burns), ribes removal (mechanical and chemical), stand rehabilitation, biological control (T. maxima), rust indexing, rust status surveys, rust damage prediction, stocking control of streams and ridgetops, and selective ribes removal.

The effective application of this arsenal will be difficult and sometimes costly, so why even try to grow western white pine. Howe and Manning (these proceedings) amply demonstrated the answer this morning. In the final analysis, however, the added value of the white pine must pay the rust management costs.

#### Current situation

What has changed since white pine management was dropped by the U.S. Forest Service in 1968 (Ketcham, et al. 1968)? To begin with, resistant pine is now a proven fact with predictable field performance a reality (McDonald, this meeting). Presumably, the overall susceptibility of the pine population has been greatly reduced by the quick death of the most susceptible individuals over almost the entire range of western white pine. Ribes and rust may be arriving at a local accommodation that can be enhanced (McDonald, this meeting). Not to be discounted is the accumulated effect of the ribes eradication program. Many fewer old growth stands supporting large accumulations of ribes seed now exist. Non-disturbance logging methods (balloon, helicopter, winter) are now more readily available. New markets that lead to shorter pine rotations are available. We have sixty years of experience with blister rust. Quantitative measures of rust hazard and the general availability of information management systems, including epidemiologic simulations (McDonald, et al. 1981) and growth projection models capable of handling detailed information needed to make an integrated rust management system workable are now available.

Forest managers in north Idaho are faced with two problems. First, what can be done with currently established stands composed of susceptible material growing on sites with a moderate rust hazard. Second, how do we install and manage stands composed of naturally or artificially selected resistant material.

The principals and methods used to attack both problems are essentially the same. The objectives of this management approach are to reduce the probability of ribes infection by aeciospores, reduce the probability of rust multiplication, and reduce probability of pine infection and rate of rust growth which then reinforces the other reductions.

#### Pine management

The management objectives for the pine host should be to increase the overall level of resistance, maintain a very large gene pool (billions of genotypes), obtain rapid stand closure, and reduce aeciospore populations. The large gene pool is obtained by aligning resistance needs to expected hazard and making widespread use of open pollinated improved and naturally regenerated material while restricting the use of highly bred populations to specific needs. Also implicit in this approach is that resistance, either natural or artificially derived, serve as the framework on which to add all harmonizing ancillary management options.

Full implementation of this integrated rust management approach would require wholesale changes in current white pine breeding programs as well as forest management practices for all species where western white pine is a possible stand component and ribes bushes might grow. More emphasis should be placed on finding trees that transmit high levels of resistance with open pollination and on determination of field performance of all sources of resistance. Also, all efforts at engineering a highly resistant western white pine population should be concentrated at one location. Basic to application is use of a rust hazard indexing system to predict probability of parent tree escape as well as progeny performance (McDonald, this meeting) so that performance of all possible resistant populations can be predicted. Also needed are cheap and reliable methods of stand rehabilitation in case some unforeseen event causes an unacceptable level of infection and rust status surveys so we would know when the unacceptable had happened. Fortunately, both indexing and status survey methods are needed to manage current plantations and natural stands of susceptible material that continue to develop but contain too much rust to be economically viable although they are a significant biological happening.

Much background information exists for development of pruning and canker excision methods for stand rehabilitation (Martin and Gravatt 1942, Stewart 1957, and Moss 1957). The natural reduction of hazard as the stand closes harmonizes with rehabilitation. The effectiveness of basal canker treatment can be seen in many currently closed stands that were treated in the early '60's. If these methods worked on susceptible populations, their effectiveness and ease of application should be multiplied on resistant populations.

New methods of rust status survey and damage prediction are under development for use in stands 10 to 25 years of age. The idea is to measure tree height, count number of whorls and number of cankers to obtain rust index; then to measure distance to girdle on bole cankers, distance to bole of branch canker nearest the bole, and diameter of bole at branch attachment. This information would be used to compute probability of new infection, predict years to death of tree, and probability of death from currently visible cankers. Such surveys could be applied to stands and/or individual trees as an aid in selecting crop trees or deciding whether or not to even try rehabilitation. The level and kind of resistance in the population needs to be accounted for because rust growth rates and probabilities of infection change with the host population. Some new possibilities are on the horizon such as defoliation of second and third year needles within one year of a heavy infection year (McDonald 1979).

### Ribes management

We should manage Ribes genes to increase resistance in a reduced population. The objective is to reduce the competitive ability of Ribes against all agents and simultaneously increase its level of resistance against Cronartium and reduce the number and distribution of Ribes plants (Moss and Wellner 1953). Understanding of the upland Ribes cycle shows how this objective can be attained. In North Idaho, 94% of the Ribes plants removed by the eradication program came from upland sites. Of these, 49% were Ribes viscosissimum and 43% were R. lacustre. Thus, the Ribes species of most serious immediate impact are R. v. and R. l. Ribes v. and R. l. accumulate seeds in the duff at the rates of 500 and 250 seeds/year/bush, respectively for about 20-30 years if normal stand closure happens. This means each bush will deposit about 10,000 or 5,000 seeds. These seeds then lose viability at the rate of 0.3% per year. If stocking is poor or the initial stocking was susceptible white pine and the Ribes population was high, a brush field could be created where the bushes will deposit for 50 to 100 years yielding up to 50,000 seeds/bush.

Considerable evidence is accumulating that shows large bush to bush variation in susceptibility to C. ribicola aeciospores and urediospores (McDonald, this meeting). Thus, it is conceivable to increase the level of resistance in local populations of ribes. This opportunity is further enhanced by the obligate outcrossing nature of ribes (Offord, Quick, Moss 1944) and its ability to store seeds in the duff. Early selective elimination of susceptible bushes should lead to a rapid accumulation of resistant Ribes seed. Populations of less than 25 per acre would be needed to apply this approach.

The important principals in managing ribes genes are: suppress ribes plant establishment, prevent seed buildup, and if possible, selectively eliminate susceptible bushes.

These objectives can be accomplished by (1) non-disturbance logging to allow light and heat to kill seeds stored in the duff before they can germinate and (2) establishment of mixed species stands designed to provide rapid stand closure and a long double rotation such that at 75 to 100 years the pine could be removed with a disturbance logging designed to germinate ribes under 50% shade of non-host species with the final cut at about 150 years. There are, of course, many other possible avenues to the same end.

### Rust management

The final objective of this rust management approach is to exercise directed control over the rust gene pool. In the first place we would not want to practice genetic overkill with either ribes or pine. Since pine is the economically important and physically largest host, it is the one where genetic overkill is most likely to occur. If we were to plant one to a few, say 25, super resistant varieties of pine on all sites, I expect we would soon find that we had applied the wrong kind of gene management to the rust. Further, we would surely find ourselves in hot water regarding some other pest, not to mention possible future genetic manipulation of the pine. The agriculturists' lessons and the wild model both tell us to maintain a functioning but low level rust population; that is, create a genetically balanced endemic situation. Such endemic systems are probably characterized by locally interacting populations of pests and hosts. If this is happening with blister rust, then we have another management consideration to contemplate. We should move to reduce the possibility of long distance spread by aeciospores. Some Ribes species and some bushes within a given species are highly susceptible and act as traps and multipliers of races of the rust that can then cause great damage locally. Our response to this threat should be the same as for management in general. All management should be directed at reducing ribes plant numbers, increasing ribes plant resistance, breaking the ribes seed accumulation cycle, and reducing the local concentration of aeciospores.



## Conclusions

In summary, managers of forests where white pine is a needed component should make all management decisions to accomplish overall reduction of ribes populations. In the long term, they should control stocking where possible on ridgetops, and along streams and swamps; survey stands older than 100 years for concentrations of ribes seeds; burn or apply herbicide to clearcuts that produce more than 25 bushes per acre to reduce ribes population to less than 25/acre; prevent the formation of brush fields and manage to reduce stand openings. Additional options are plant spacings and species mixes to cause rapid stand closure; execute partial cuts to cause elimination of stored seed and prevention of seed accumulation; align resistance and hazard index to maximize genetic breadth of pine; and finally, rehabilitate stands and selectively remove susceptible ribes where economically feasible and biologically desirable. The consistent application of these management practices will return white pine to a productive role in western forests, make effective use of all sources of resistant pine, minimize future problems of racial variation of C. ribicola, and maximize opportunities for future improvement of growth and other traits of western white pine.

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Using Rust Resistance in Forest Management  
(Panel Discussion)

by

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In considering the fusiform rust situation in the South, it is important to remember that we are dealing with native hosts and a native pathogen. Thus, conditions do not parallel those with white pine blister rust, which is so damaging in the Northwest. Fusiform rust was first identified in 1896, and during the first half of this century it was more of a mycological curiosity than a problem to forest land managers. The pathogen and the host had reached a state of equilibrium, and the losses that occurred were tolerable. After World War II, when more intensive forestry was started in the South, things began to change. Planting and other intensive forest management practices created a favorable environment for rust. Intensive forestry really got into high gear in the Southern United States during the 1950's, the years of the soil bank program. In 1959, the peak year, 1,680,000 acres were planted to pine in the South.

By the late 1950's it was obvious to everyone concerned with forestry in the South that fusiform rust was a major and growing problem. Its severity increased with every advance in intensive forest management. Rust infects more trees in planted than in natural stands. The more intensive the site preparation, the more rust can be expected. Fertilizer application speeds growth of young trees, but it also makes them more susceptible to the disease. Control of forest fires, which at one time did much to control the oak alternate hosts, also results in more inoculum to infect the pines. Mechanical site preparation, which leaves windrows of debris at intervals of 100 years or so provides relatively protected strips of oak sprouts evenly distributed throughout pine plantations. In other words, we have

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created ideal situations for the pathogen. By the mid-1960's the rust problem was well recognized, and various companies and states started programs to develop speciality orchards for the production of rust resistant material for use in high hazard areas. We began such a program at the Southeastern Station in 1967 in close cooperation with the Georgia Forestry Commission.

Unfortunately for forest land managers, neither the geneticists nor the pathologists had much help to offer at that time. There simply were no resistant materials available for planting. We were able to tell forest land managers some of the things that might cause an increased level of rust, such as planting. However, most of these things were involved in the company land management plans, so there was little that the forester could do about it. Thus, forest land managers had to make key decisions about fusiform rust without solid information, and within an area that we refer to as the fusiform rust zone, rust had become a key element in forest management. Decisions such as which species to plant, the intensity of site preparation, the planting spacing, the type and intensity of thinning, rotation age, and even the final product to be produced were strongly influenced by the severity of fusiform rust. One company forester in southeastern South Carolina decided to stop planting slash pines when he found that most of his 5- to 10-year-old stands were so severely damaged by rust that salvage was the only sensible alternative. He harvested what little pulpwood was present and switched to loblolly pine in all of his reforestation programs. Loblolly pine is not resistant or immune to this disease, but it seems to tolerate the disease a little more successfully than does slash pine in South Carolina.

By 1970 many foresters were applying the findings of Wells and Wakeley, who showed that loblolly pines around the periphery of its natural range provided resistance to the disease. Resistant sources were Livingston Parish in Louisiana, east Texas, Arkansas, and the eastern shore of Maryland. Foresters could buy bulk

seed lots, particularly from Livingston Parish, and obtain some gain in rust resistance over other commercially available sources.

One forest manager from eastern Georgia decided in 1973 to plant nothing but Livingston Parish loblolly. He was unable to produce a crop of pulpwood planting the material that was being furnished him from the seed orchards owned by his company. He knew he was taking a chance using material that far from its source but, as far as he was concerned, things were already so bad that he had very little to lose. In the second year of this planting program, the company bought over 10 tons of Livingston Parish seeds. As of last year the program seemed to be working. The early plantations were in their 8th and 9th years, and although fusiform rust is a bit higher than anticipated, they will produce reasonable crops of pulpwood on these relatively high rust hazard sites. This example demonstrates an important point. Forest land managers--at least the kind we have in our area--are going to do something when they are faced with a problem of this magnitude. They take the best available information--even if that information is mainly from personal observations--and they make a decision.

We are monitoring the rust population where extensive plantings have been made with seeds from resistant geographic areas, primarily Livingston Parish. We do not know whether there will be an increase in virulence of the pathogen in these plantings where, presumably, selection pressure is being exerted on the rust organism to overcome the resistance in the host. These geographic seed sources are bulk seedlots and are certainly very diverse genetic material. Also, even after all of the planting done in the South over the past 30 years, less than 25% of the total loblolly pine inventory is in planted pines. Therefore, at least 75% of the loblolly pines are natural, unselected material, which in many areas is largely susceptible. Selection pressure on the pathogen should never reach the level found with wheat rust, or some other agronomic crops.

While these geographic seed sources were being utilized, many companies and states in the rust area were establishing speciality orchards for production of rust resistant seeds. Most occupy 4 to 5 acres, but the one we have established with the Georgia Forestry Commission is 60 acres, one of the largest of this type. Primarily these orchards are formed by grafting scions taken from the most resistant selections available in the South. Unfortunately, the number of highly resistant selections is relatively limited, particularly for loblolly pine. The best estimate that I was able to make several years ago was that there were less than two dozen highly rust resistant loblolly clones available for utilization in the entire South. Of course this excludes the bulk seed lots from specific geographic areas. I have seen very little over the past few years to make me think that we should change that estimate. However, there are other selections with intermediate levels of resistance which probably could be added to that total.

Many rust resistant orchards are in the early stages of production. Seeds of resistant stock either are or shortly will be available for relatively large plantings. If our greenhouse test results are indicative, the seeds from these orchards should be at least as resistant as the geographic seed-source material. At long last we are now offering an attractive alternative to forest managers who are trying to produce a crop in very high rust hazard areas.

In the South there is no choice between vertical or horizontal resistance, because vertical resistance appears to be absent from materials that are now being established in seed orchards. We must now decide on the best deployment for the material that we now have available and on the best philosophy for the establishment of rust resistant orchards. Many people would like to have as broad a genetic base as possible to avoid heavy dependence upon any particular selection or clone. Virulence is sharply increased by collecting inoculum from a specific pine family and reinoculating seedlings of that same family. These increases in virulence

in some cases have been truly startling. On the other hand, we all recognize the differences in our situation from those of the annual crop pathologist and geneticist, like those working with wheat. If plantations are able to get to age 6 or 8 without having a devastating rust infection, they can probably be carried for an entire rotation. A family-specific population of the rust probably will seldom sporulate on a given resistant pine population quickly enough to cause serious damage. Since the first sporulation takes place within 5 years, there is an outside possibility that such family-specific populations could arise and do considerable damage if weather conditions were extremely favorable for the rust. Since years of severe rust infection occur in our area only every 3 to 5 years, however, it is quite likely that the plantation would get through to a relatively large size before the new virulent rust became the majority of the rust population in that area.

Another point to consider is whether we should try to produce rust-resistance material in an orchard with relatively few genotypes for resistance, or try to develop orchards with as many different sources of resistance as possible. The options here are somewhat similar to those considered by the wheat breeders. Do you use one good resistant selection for as long as it will last, while holding the other sources of resistance in reserve? When the rust begins to overcome that resistance, you switch to another source. The alternative is to try to keep the rust incidence relatively low by including in the orchard a broad and generous mix of all of the best sources available. Frankly, I am not certain which is the best approach, but as of now, most people have tended toward the latter, that is, the mixture of all of the sources that are currently available.

The method of seed orchard establishment is another question. The seedling seed orchard is quite different from the clonal orchard that has been used in most of the Southern United States. All of the large tree improvement corporatives in this area advocate clonal orchards. The seedling seed orchard, however, is tailor-



made for the utilization of survivors artificial inoculation tests. It therefore offers an additional level of resistance to the material, and may considerably broaden the genetic base of resistance. The pollen parents of the seedlings that are tested for resistance represent some of the best selections from seed orchards throughout the entire area. Therefore there is no question that the formation of seedling seed orchards utilizing survivors of artificial tests offers a new dimension to the development of rust resistant orchards. Clonal orchards also have advantages--both parents are known, and the quality of material is highly predictable.

Decisions made relating to these questions will have a direct bearing on the progress of rust control programs in the South and, in turn, on the future of timber supplies from this highly productive region.

OVERVIEW OF RESEARCH IN TREE IMPROVEMENT

by

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The major purpose of this meeting started out to be resistance in various species to white pine blister rust. It was expanded to include other rusts, principally fusiform, and then to include insects. I was asked to give an overview of research in tree improvement. With a request like that, I felt that I had to discuss more than research dealing with pest resistance in tree improvement because pest resistance is just a very small part of the tree improvement picture. We could produce resistant cultures to almost any pest you could name, but they may or may not be of any use.

I tried to write this paper several times. It was very difficult. Basically I found that I really don't know what is going on. By the time I got around to writing this paper, I didn't have time to do the necessary literature review. I would like to have had, at least for the Forest Service Research Stations, a list of all the active studies on genetics. And I think it would also be useful to tabulate the last 5 years of publications. This can be easily completed by going over the attainment reports (a copy can be obtained from each Station by writing the Station headquarters).

I think this would be very valuable for the tree breeders because they would then know that someone is working on their problems. Or, if their problems are not getting attention, they would know they would have to speak up. Researchers don't always know what needs to be done. More important, researchers don't always work on priority problems, i.e., those things researchers want to work on may not have immediate practical application.

However, I do have an opinion about where I think research is today. The direction in both research and tree improvement has changed. Rangewide provenance tests, species introductions, and hybridization were high on the list 20 years ago. Today there is much more research within regions, so now the provenance tests are aimed at trying to understand the patterns of genetic variation within a fairly limited geographic area. Genetic gains are those that can be made by selecting within species, and most of us have come to realize that native species have greatest potential--the grass is greener on this side of the fence.

I like to divide research into two areas. One is the research needed to do the immediate tree improvement job. These would be knowledge needs for seed transfer rules, establishing breeding units, genetic variation of desired traits, genetic gains, and seed orchard technology. The second area deals with the more basic aspects of genetic research. Tissue culture, taxonomic research using not only morphological traits but with phenolics, terpenes, isozymes, and physiological genetics of various kinds. These kinds of research have tremendous potential, and the payoffs from them will eventually be very high. However, they do little for the practicing tree improver who must make decisions today. So, most of this paper will deal with research on immediate practical problems.

In talking to practicing foresters, I hear several questions that deal with genetics:

1. How far can I transfer seed?
2. What kind of an improvement can I expect if I leave these seed trees?
3. How much gain can be made with plus trees?
4. When am I going to get improved seed?

5. How can I get rust resistant white pine stock?
6. What kind of seed orchard is best?
7. Can I get ponderosa pine resistant to mistletoe, lodgepole pine resistant to gall rust, or mountain pine beetle or Douglas-fir to spruce budworm? When are you going to work on resistant to root rots? And so on.

These questions, more or less, tell us what tree improvement is all about. There are all kinds of way to skin a cat. Depending on species and area of the country, a researcher could start at various points. Unfortunately tree improvers need almost all the data right now. But there are priorities.

In my view, the first question to work on is seed transfer rules including breeding units or zones. Out West this is of tremendous value whereas in the East, especially the southeast, seed transfer or even breeding units don't seem to pose much of a problem. Figure 1 illustrates what I am referring to. This is a map of average growing season (number of days between 32° F). In the East, the lines are very broad, but look at the West. Growing season changes radically over very short distances. For western Washington, Oregon, and California the changes more or less go from west to east. For the interior, the changes are much more jumbled, although there is still a noticeable west to east change. For example, eastern Washington and northern Idaho experience a high maritime influence but this changes after crossing the Bitterroots to more continental and becomes largely continental after crossing the Continental Divide. The extremes in all areas are high--from nearly 300 days in Washington, Oregon, and California; 184 days at Lewiston, Idaho, to 3 hours and 15 minutes in all these states at high elevation. Of course, we don't grow trees way up there nor do we grow them at Lewiston because it's too dry. But this certainly should indicate the problem.

FROST OCCURS IN LESS THAN HALF THE YEAR ALONG IMMEDIATE COASTS OF NORTHERN 70 DEG OF CALIF. AND 30 DEG ALASKA (70 DEG CIRC 1110).

IN ALASKA SHOW COASTS OF YEAR IN NORTH SOUTHERLY ALSO ALASKA (70 DEG CIRC 1110).

IN HAWAII NO FROST IN MOUNTAIN ABOVE 5,000 FEET. HAWAII (70 DEG CIRC 1110).

FROST OCCURS IN LESS THAN HALF THE YEAR.

FROST OCCURS IN LESS THAN HALF THE YEAR.

CAPTION SHOULD BE USED IN INTERPRETATION OF THIS CONTINENTAL MAP. READ COMMENTS ON THE LOW LIMITS OF FROSTING AND DROPPING AND ALSO ALLEGEDLY BEARS ON LOW TYPE OF SOIL. (70 DEG CIRC 1110).

Based on Period 1921-50.

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Most of the studies that have been established for purposes of defining seed zones have been intraregional, long-term provenance tests. Some highly successful tests have been established, especially in Scandinavia with Scots pine, Norway spruce, and lodgepole pine. As Bob Campbell showed, two basic requirements of these kinds of tests are that there be enough (like 50) plantations along major lines of environmental variability, usually latitude and elevation, and that the tests be intensively managed. Personally, I have not seen any tests in this country that qualify as an adequate seed zoning test.

There are other ways to get the kind of data needed for seed zoning. It is the area of work that is called genecology, i.e., the study of adaptive variation. This kind of work is based upon research methods of horticulturists, beginning with Clausen, Keck and Heisy. By closely controlling extraneous environmental variation, genetic differences can be readily detected. It is a lot like the field provenance tests; however, tests differ because people are trying to gather and analyze data in terms of how genetic characters interact with the environment, basically the growing season. Also, adaptation to cold is tested in the laboratory to determine frost or cold hardiness at various times of the year in respect to the growing season. The "field" portion of these tests differ only in the density of planted seedlings and the length of time the test is maintained. It is also important to use statistical procedures that permit an understanding of the data.

Most common statistical procedures end up telling us that there is a difference. What is important is to quantify or apply the differences in a meaningful way across the landscape. Some researchers that I know that are doing this kind of work in this country are Bob Campbell and Frank Sorenson at PNW, and Jerry Rehfeldt at INT.

The same data is used to establish seed transfer rules and breeding zones. But there is a basic difference. A breeding zone must be a specific piece of ground over the landscape because the selected trees within the unit will form the base for the breeding program. On the other hand, since STR apply to artificial regeneration from the seed collected from a particular stand, you only need to know how far to move, i.e., so many feet of elevation, degrees latitude, etc. (See Rehfeldt 19 for an example.) The nice thing about this is that no lines are needed and this should simplify this phase of the planting program.

The real trick in establishing STR and BZ is to know how much risk to take. I think one should first establish the rules and zones by decreasing the rules or size until the genotype-environment interaction is zero. This would establish the minimum rules and size. And then determine the amount of gain that can be made from the breeding work. The gain minus losses from negative adaptation resulting from expanding the rules and size would represent the maximum. The true breeder must then balance gains and losses to establish optimum seed transfer rules and breeding zones. Long-term tests are needed to make adjustments for the next breeding cycle.

The next area of genetic research to discuss is that large area dealing with plus tree selection, progeny testing, selection, and gain. This is all straightforward classical genetics. There is a lot of good work going on, here and there, and I don't think we need to discuss it much except for one point--how soon can you use data, that is, when is the data from a progeny test valid? The historical answer has been half rotation. I have seen very little data (none of it very good) that supports this long period of wait. Most available data is confounded by genotype environment interactions, a very small sample, or extensive damage to the trees. For example, a broken leader that was 3 to 4 feet long has an effect on several years growth. Some workers talk of large flip-flops in ranking that would cause large errors in "early" selections. Without confounded data, I just don't see how that can happen; not, at least, with intolerant conifers. Height growth for an intolerant conifer is a fitness character. If trees like white pine, lodgepole pine, western larch, and Douglas-fir haven't made their move by 10 to 15 years, they are out of luck. So even if there is a small percentage of trees that start slow and end fast, I don't want them. I want those trees that start fast and end up fast.

There have been a couple of reviews on juvenile-mature correlations and a section of the IUFRO meeting in Stockholm covered this area. To me, the consensus before 1970 was for early selection. After 1970, the difficulties of early selection were overemphasized. The literature that I have seen still indicates the consensus is still for early selection, but there is a lot of confusion. My assumption is that the correlation is high, but if a test reveals a low correlation, it's a screwed up test and I would try to determine the causal agent, e.g., seed size, broken tops, gopher damage, root rots, shoot moths, and others.

Another thing that has always bothered me was that people argue against early selection and then go do it. However, early selection on their long-term field tests. Why not set up a specific early selection trial that minimizes environmental variances? This will then provide much better data. And since it will be at minimum spacing, it will be much cheaper even with intensive management.

An early selection trial should be established and maintained as follows:

1. You have already determined your breeding units. This, then, minimizes the genotype-environment interaction in evaluation trials.
2. Choose the best growing site for each of your breeding units;

3. Establish a high-density (3' x 3') in the Northern Rockies, highly maintained evaluation plantation with a life expectancy of 10 years;
4. Intensively manage the site; no cows, elk, deer, gophers, root rots, bug spores, etc.
5. Keep records of seed weight (at least for another year).
6. Obtain genetic correlations among production and adaptive traits so that indices can be constructed to achieve genetic gains without altering natural fitnesses.
7. Obtain genetic correlations among "traits".

The production side of forest genetics is advancing on many fronts. Tissue culture and flower-inducing hormones are two of the bright stars. Eventually those tools will be available for all species. Methods for detecting graft incompatibility are available now. This should decrease some of the fears of grafting. Seed and cone insects are going to cause us problems. We need more research in this area. Seed orchard management, i.e., pollen, seed production, watering, fertilizer, and pruning need more research attention at the species level. Generalities are known; but responses of each species in a particular orchard site are not.

My last topic is pest resistance and since this area is going to be covered from many different aspects during the next 4 days, I will not say much here. However, there are several points that need to be emphasized.

1. Resistance breeding to various pests will be a constant part of all breeding programs. For example, tree improvement with any of the white pine will have to include breeding for resistance to blister rust.
2. Special tests must be established to subject selected trees to various pests to make sure that selection does not include susceptibility.
3. All pest management procedures must be considered along with resistance in each of the breeding programs.
4. A breeder must be a Jack-of-all-trades. Pest management must be as important to him as selection for growth and form.
5. Maintenance of resistance to native pests will be a lot easier as compared to reintroducing resistance.

There is quite a lot of research being done on pest resistance throughout the country. Most of it is on the big problems: fusiform rust and white pine blister. A lot of it is opportunistic. We see the effect, take the data, and publish a paper. Maybe this is where things have to stay for awhile. But it also seems to me that somehow we have to start to make plans for the catastrophies that are going to happen. Tests with potential pests should be included in all the Regional tree improvement plans. For example, I don't think there is any doubt that the hard pine stem rusts can be extremely damaging. Plans on ponderosa pine and lodgepole pine should include tests with, at least, western gall rust. Seems to me most tree breeders are way too optimistic. The agronomic literature certainly indicates that this is foolhardy.



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